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BULLETIN

OF

ENTOMOLOGICAL RESEARCH.

ISSUED BY THE IMPERIAL
INSTITUTE OF ENTOMOLOGY.

EDITOR : THE DIRECTOR.

VOL. 28.

LONDON :
THE IMPERIAL INSTITUTE OF ENTOMOLOGY,
41, QUEEN'S GATE, S.W.7.
1937.

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ERRATA.

Page 6, line 5, for " *Lophacrama phaenichlora* " read " *Lophocrama phoenichlora* "

,, 9, 11 lines from end, for " *Rhynchophora* " read " *Rhynchophorus* "

,, 109, 13 lines from end, for " (Hegh 1929, p. 237) " read " (Hegh 1929, p. 264) "

,, 146, line 12, for " Res. Un. Afr." read " Res. Un. S. Afr."

,, 322, line 6, for " known " read " unknown "

,, 395, line 6, for " April 1934 " read " April 1936 "

,, 405, line 24, for " (*Mysomyia*) " read " (*Myzomyia*) "

,, 409, 7 lines from end, for " as *fragaefolii* " read " as *fragariae*. These specimens seem to us to be identical with specimens of *fragaefolii*."

,, 412, line 12, for " *Capitophorous* " read " *Capitophorus* "

,, 414, line 4, for " apterae " read " viviparae "

,, 426, line 1, for " 1932–33 " read " 1933–34 "

,, 476, 22 lines from end, for " Subfamily BARIDINAE " read " Subfamily CRYPTORRHYNCHINAE "

,, 484, 8 lines from end, for " *Hoplandothrips* " read " *Hoplandrothrips* "

,, 500, line 23, for " reaction " read " reaction induced by high temperature "

,, 514, line 5, for " *Pseudololna* " read " *Pseudotolna* "

DATES OF PUBLICATION IN PARTS.

Part **I**	pp. 1–170	...	**30** March **1937.**
Part **II**	pp. 171–340	...	**2** July **1937.**
Part **III**	pp. 341–524	...	**12** October **1937.**
Part **IV**	pp. 525–642	...	**20** December **1937.**

IMPERIAL INSTITUTE OF ENTOMOLOGY.

BULLETIN

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ENTOMOLOGICAL RESEARCH.

VOL. 28. 1937.

INCIDENCE OF ATTACK BY THE PIN-HOLE BORER, *PLATYPUS CYLINDRUS*, F., IN ENGLISH ASH.

By RONALD C. FISHER, Ph.D.,

Entomology Section, Forest Products Research Laboratory, Princes Risborough.

(PLATE I.)

Pin-hole borer damage to timber, caused by beetles of the families SCOLYTIDAE and PLATYPODIDAE, is associated chiefly with recently felled logs and occasionally with standing trees which are in an unhealthy condition. Information collected within recent years by the Forest Products Research Laboratory, Department of Scientific and Industrial Research, suggests that attack in standing trees may, however, be of more frequent occurrence than has been commonly supposed. In this connection, an interesting case of damage to English ash by the Platypodid beetle, *Platypus cylindrus*, F., is worthy of record.

During conversion in January, 1936, of a number of ash logs, winter-felled 1935–36, at a sawmill in Shropshire, the sapwood of one log was found to contain numerous insect tunnels, although no external evidence of their presence had been apparent before sawing. The occurrence of this uncommon defect in only one out of several logs attracted the attention of the firm concerned, who sent samples of the attacked timber to Princes Risborough for examination and report.

The insect tunnels were typical of pinhole borer damage, the dark stain usually associated with this type of defect, and due to fungus, being present in their immediate vicinity (Plate I, fig. 1). The species of pin-hole borer concerned was identified from remains of dead beetles in the tunnels as *Platypus cylindrus*, F.; no living insects were found. The position of the tunnels, which penetrated the sapwood in a radial direction, was of special interest since they came to an end some distance from the surface of the sapwood, in which entrance-holes were not present. Moreover, the outer end of the tunnels was closed by a plug of wood tissue.

Specimens were examined by Mr. B. J. Rendle, Officer-in-charge of the Wood Structure Section of the Laboratory, to whom the writer is indebted for notes on the structure of this abnormal wood tissue. The tunnels terminated at a depth within the sapwood equal to the growth of the tree during the four years prior to felling, *viz.* 1931–1935 ; in other words, in the spring of 1931 new wood formed by the stem cambium grew over entrance-holes at that time present in the surface of the sapwood, the initial attack having taken place in the summer of 1930. During the growth of this new wood in 1931, a cylindrical plug of traumatic parenchyma tissue was also formed to fill up the entrance of the tunnel to a depth of 3–5 mm. (Plate I, fig. 2). In subsequent years—1932 to the date of felling in the autumn of 1935—successive annual rings were added so that the insect tunnels became completely overgrown and incorporated within the sapwood of the tree. Had the tree not been felled this sapwood would in due course have changed to heartwood, the tunnels remaining as a permanent record of pin-hole borer attack during the earlier life of the tree. Such a means of occluding insect tunnels is similar to that described by Neger (1909) in connection with the healing of injury caused to fruit trees by the Scolytid, *Xyleborus dispar*, F.

A study of the width of the annual rings immediately before and after 1930 showed that prior to that date the tree was more vigorous in growth and the annual increment greater than in subsequent years. It would appear that the vigour of the tree was checked at some time after the completion of the 1929 annual ring, the width of the 1930 ring being markedly less. It is probable, therefore, that some factor or factors came into play in 1929–30 which adversely affected the growth of the tree, rendering it liable to attack by *P. cylindrus*. It is interesting to note that, although the tree was able to overcome the attack, successfully occluding the insect tunnels, it apparently did not regain its former vigour, since the annual increment in the years following 1930, the year of infestation, was considerably less than in those preceding the attack. It seems probable that the factors which affected its growth in 1930 continued to operate, but although sufficient to render the tree temporarily susceptible to attack, were not so severe as to prevent recovery.

Unfortunately, no information on the past history of the log could be obtained, so that it is not possible to give any definite observations in support of these conclusions. It seems reasonable to conclude, however, that change in environmental conditions, *e.g.*, drought or a lowering of the water-table, affecting the health and vigour of the tree play an important part in determining its degree of susceptibility or resistance to pin-hole borer attack. So far as infestation by *P. cylindrus* is concerned, this record of damage confirms Escherich's (1923) statement that this beetle can attack standing timber, but its presence does not necessarily mean that the infested tree is doomed as was believed by Hubbard (1897), who writes :

> " The species of *Platypus* do not attack trees in health. They are attracted by the fermenting sap of dying or very badly injured trees. The death-rattle is not more ominous of dissolution in animals than the presence of these beetles in standing trees. If the timber attacked by them is to be saved even for firewood the sooner it is cut down and seasoned the better."

The occurrence of pin-hole borer damage during the life of a tree and the successful occlusion of the tunnels by the growth of subsequent years is of special interest in relation to recent observations on insect attack in new timbers from different parts of the Empire. In this connection the presence of pin-hole borer damage has become of considerable importance, since such extensive injury is so frequently caused to freshly felled timber in tropical countries that its market value is seriously affected. Not only do these insects attack felled timber but in some cases, *e.g.*, meranti (*Shorea* sp.) in the Federated Malay States, apparently sound logs are found on conversion to be extensively tunnelled in the heartwood (Browne, 1935). Such a condition is comparable to that of the ash showing the *Platypus* damage described above, and is the result of past infestation at some time during the life of the tree.

Few observations have been made on pin-hole borer attack in felled timber or standing trees and there is a great need for information on the food requirements of these important insects and upon the factors which determine the suitability of timber for infestation. Until such knowledge is available the possibility of preventing this type of insect defect in timber must remain unknown.

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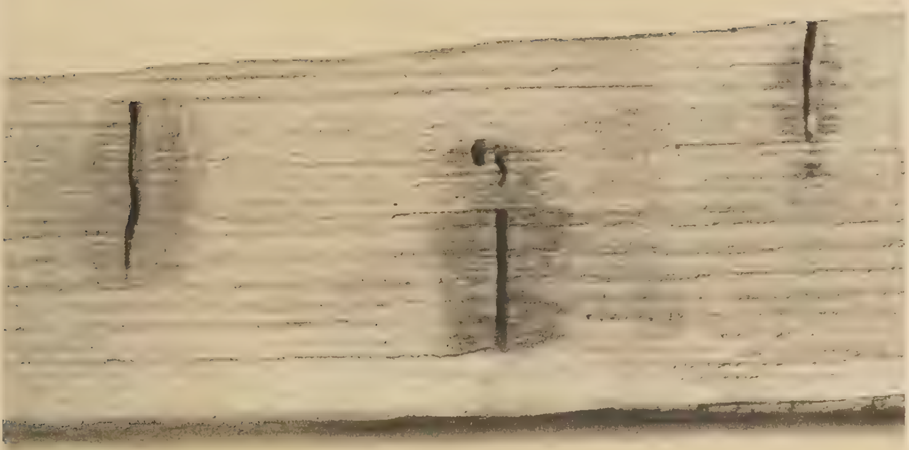

Fig. 1. Tunnels of *P. cylindrus* in ash showing associated dark stain due to fungus. (Natural size).

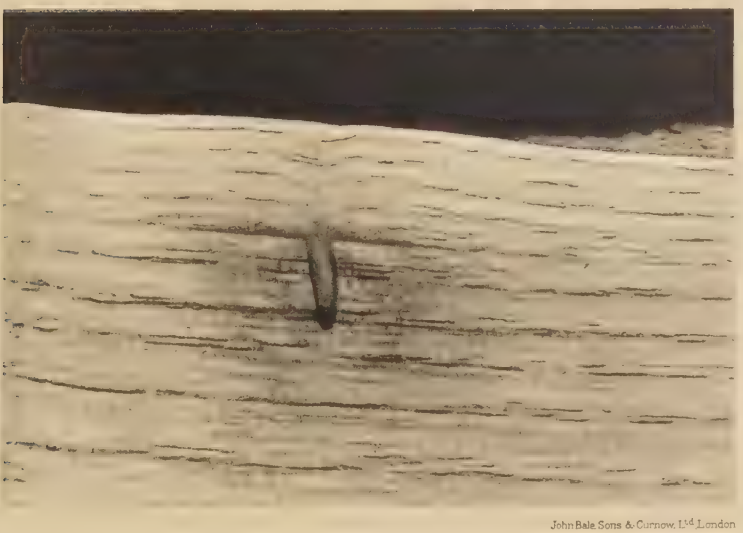

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Fig. 2. Occluded tunnel of *P. cylindrus* in ash showing plug of traumatic parenchyma tissue. (X2 approx.).

FURTHER NOTES ON THE FOOD-PLANTS OF NIGERIAN INSECTS. IV.

By F. D. Golding, M.A., F.R.E.S.

In 1927, 1931 and 1935, the writer published three papers on the food-plants of Nigerian insects in this Bulletin (**18,** pt. 1 ; **22,** pt. 2 ; and **26,** pt. 2). The present paper contains additional data obtained between November, 1934, and March, 1936. On the advice of the Botanical Section, Nigerian Agricultural Department, certain changes have been made in the nomenclature of economic plants. In the previous papers the nomenclature employed in the Kew Bulletin entitled " The Useful Plants of Nigeria " was adopted. The following list shows the English or native name of the crop and the old and new scientific names.

English or native name	Old nomenclature	New nomenclature
Sweet Orange	*Citrus aurantium*	*Citrus sinensis*
Grapefruit	*C. decumana*	*C. paradisi*
Tangerine	*C. nobilis*	*C. nobilis* var. *deliciosa*
Lime	*C. medica* var. *acida*	*C. aurantifolia*
Gbanja Kola	*Cola acuminata*	*Cola nitida*
Abata Kola	—	*C. acuminata*
Cowpea	*Vigna sinensis* *V. catjang*	*Vigna unguiculata*
Ishan Cotton	*Gossypium vitifolium*	*G. barbadense*

In the paper published in 1927 the Coreid bug, *Anoplocnemis tristator*, F., was erroneously named *A. testator*, F.

The writer wishes to acknowledge his indebtedness to the Imperial Institute of Entomology and the specialists of the Department of Entomology in the British Museum for identifying the insects mentioned.

Name	Food-plants	Part attacked	Month of appearance	Locality and remarks
	LEPIDOPTERA			
NYMPHALIDAE—				
Leucosticha daedalus, F.	*Terminalia catappa*	Leaves	Nov.	Ibadan
ARCTIIDAE—				
Diacrisia screabile, Wllg.	*Gloriosa superba*	,,	Aug.	,,
HYPSIDAE—				
Asota speciosa, Drury ...	*Ficus asperifolia*	,,	Nov.	,,

Name	Food-plants	Part attacked	Month of appearance	Locality and remarks
	LEPIDOPTERA—*cont.*			
NOCTUIDAE—				
Othreis fullonica, L. ...	*Citrus paradisi*	Fruit	May	Ibadan adults
Achaea mormoides, Wlk.	,, ,,	,,	,,	,, ,,
Brithys pancratii, Cyr. ...	*Hippeastrum equestre*	Leaves	,,	,,
Lophacrama phaenichlora, Hmps.	*Theobroma cacao*	,,	Sept.	,,
Anomis leona, Schaus ...	,, ,,	,,	Sept.	..
	Cola nitida	Pods	,,	,,
Prodenia litura, F. ...	*Vigna unguiculata*	Leaves	Nov.	,,
	Nicotiana tabacum	,,	Dec.	,,
Phytometra rutilifrons, Wlk.	*Nicotiana tabacum*	,,	July	Ilesha
LYMANTRIIDAE—				
Dasychira quinquepunctata, Mösch.	*Chrysophyllum africanum*	,,	Oct.	Ibadan
D. proleprota, Hmps. ...	*Cola acuminata*	,,	Nov.	,,
LASIOCAMPIDAE—				
Leipoxais sp.	*Ricinus communis*	,,	Aug.	,,
SATURNIIDAE—				
Bunaea rhodophila, Wlk.	*Mucuna aterrima*	,,	July	,,
PYRALIDAE—				
Sylepta balteata, F.	*Spondias lutea*	,,	,,	,,
S. retractalis, Hmps.	*Theobroma cacao*	,,	Oct.	,,
S. semilugens, Hmps.	*Cola nitida*	,,	Oct., Dec.	,,
S. polycymalis, Hmps.	,, ,,	,,	,,	..
Terastia meticulosalis, Guen.	*Erythrina umbrosa*	Stem-borer	July	,,
AEGERIIDAE—				
Aegeria alenicola, Strand	*Cola nitida*	Moribund trunk	Jan.	,,
EUCOSMIDAE—				
Argyroploce leucotreta, Meyr.	,, ,,	Wall of pod	Nov.	,,
	RHYNCHOTA			
PENTATOMIDAE—				
Atelocera raptoria, Germ.	*Gossypium barbadense*	Petiole	Oct.	,, adults
	Vernonia tenoreana	Stem	July	,, ,,
	Mangifera indica	Shoot	Aug.	,, ,,
Macrina juvenca, Burm.	*Imperata cylindrica*, var. *thunbergii*	Midrib of leaf	,,	,, ,,
Nezara viridula, L.	*Sesamum radiatum*	Pods	,,	,, ,,

Name	Food-plants	Part attacked	Month of appearance	Locality and remarks
	RHYNCHOTA—*cont.*			
PENTATOMIDAE—*cont.*				
Aspavia armigera, F.	*Sesamum radiatum*	Pods	Nov.	Ibadan, adults
Halyomorpha annulicornis, Sign.	,, ,,	,,	Aug.	,, ,,
	Tephrosia candida	,,	Sept.	Umuahia, adults and nymphs
Platynopus rostratus, Dru.	*Solanum melongena*	Leaves	Oct.	Ibadan, adults
PLATASPIDAE—				
Coptosoma marginella, Dall.	*Mucuna aterrima*	Shoots	Nov.	,, ,,
	Tephrosia candida	,,	Oct., Nov.	,, ,,
C. nubila, Germ.	*Zea mays*	Leaves	Oct.	,, ,,
COREIDAE—				
Mygdonia tuberculosa, Sign.	*Newbouldia laevis*	Shoots	,,	,, adults and nymphs
Plectrocnemia oblongipes, F.	*Mangifera indica*	Petiole	Aug.	Ibadan, adults
Anoplocnemis curvipes, F.	*Vernonia amygdalina*	Shoots	Jan.	,, adults and nymphs
	Citrus paradisi	Shoots	Oct., Nov.	,, ,,
	Gliricidia maculata	,,	Feb.	Ibadan, adults
A. tristator, F.	*Lonchocarpus cyanescens*	,,	,,	,, ,,
	Mangifera indica	Midrib of leaf	July	,, ,,
Leptoglossus membranaceus, F.	*Citrus sinensis*	Fruit	May	,, ,,
	C. paradisi	,,	,,	,, ,,
	Passiflora foetida	,,	July	,, adults and nymphs
	Cucumis sativus	Shoots	Aug.	Ibadan, nymphs
	Trichosanthes anguina	Shoots and fruit	,,	,, adults and nymphs
Mirperus torridus, Westw.	*Hibiscus sabdariffa*	Midrib of leaf	,,	Ibadan, adults
	Desmodium velutinum (lasiocarpum)	Pods	Nov.	,, adults and nymphs
Riptortus dentipes, F.	*Desmodium mauritianum*	,,	July	Ibadan, adults
	Tephrosia candida	,,	Aug.	,, ,,
	,, ,,	Buds and shoots	March	,, ,,
LYGAEIDAE—				
Chauliops rutherfordi, Dist.	*Calopogonium mucunoides*	Leaves	July	,, adults and nymphs
	Desmodium mauritianum	,,	Aug.	,, ,,
	Gossypium barbadense	,,	Oct.	Ibadan, adults
	Vigna unguiculata	,,	,,	,, ,,
Graptostethus rufus, F.	*Tephrosia candida*	Buds	Sept.	Onitsha, adults

Name	Food-plants	Part attacked	Month of appearance	Locality and remarks
	RHYNCHOTA—*cont.*			
CAPSIDAE—				
Sahlbergella theobroma, Dist.	*Citrus paradisi*	Shoots	July–Dec.	Ibadan, adults
			Sept.–Nov.	,, nymphs
	C. sinensis	,,	Oct.	,, adults
	C. limonia	,,	July	,, ,,
Helopeltis bergrothi, Reut.	*Spondias lutea*	,,	,,	,, ,,
	Anacardium occidentale	,,	Aug.	Ibadan, adults and nymphs
Halticus tibialis, Reut.	*Calopogonium mucunoides*	Leaves	,,	Ibadan, adults
	Hibiscus esculentus	,,	Oct.	,, ,,
	Vigna unguiculata	,,	,,	,, ,,
Lycidocoris mimeticus, P. and R.	*Morinda lucida*	,,	,,	,, ,,
TETTIGOMETRIDAE—				
Hilda undata, Wlk.	*Citrus paradisi*	Young leaves	July, Oct.	Ibadan, adults and nymphs
	Tephrosia candida	,,	Mar.	,, ,,
CERCOPIDAE—				
Ptyelus grossus, F.	*Citrus paradisi*	Shoots	July	Ibadan, nymphs
	Tephrosia candida	,,	Sept.	Umuahia, adults
Poophilus adustus, Wlk.	*Gossypium barbadense*	Leaves	,,	Ibadan, adults
ALEURODIDAE—				
Bemisia goldingi, Corbett	,, ,,	,,	July–Mar.	,, ,,
B. nigeriensis, Corbett	*Manihot utilissima*	,,	Jan.–Dec.	,, adults and nymphs
	M. palmata var. *aipi*	,,	,,	,, ,,
COCCIDAE—				
Pseudococcus brevipes, Ckll.	*Ananas sativus*	Stems	Oct.	Agege, adults and nymphs
	COLEOPTERA			
CETONIIDAE—				
Pachnoda cordata, Drury	*Solanum melongena*	Stems	Aug.	Ibadan, adults
	Rosa sp.	Flowers	Sept.	Oshogbo, adults
P. marginella, F.	*Citrus sinensis*	,,	Nov.	Ibadan, adults
Glycyphana sanguinolenta, Oliv.	*Tephrosia candida*	,,	Mar.–Apr.	,, ,,
Diplognatha gagates, Först.	*Solanum melongena*	Shoots	Aug.	,, ,,
RUTELIDAE—				
Popillia dorsigera, Newm.	*Hibiscus rostellatus*	Flowers	Nov.	,, ,,
MELOLONTHIDAE—				
Pseudotrochalus concolor, Kolbe	*Citrus limonia*	Leaves	July	,, ,,
	Bixa orellana	,,	Aug.	,, ,,

Name	Food-plants	Part attacked	Month of appearance	Locality and remarks
	COLEOPTERA—*cont.*			
NITIDULIDAE —				
Carpophilus humeralis, F.	*Ananas sativus*	Fruits	Jan.	Agege, adults
BUPRESTIDAE—				
Pseudagrilus leonensis, Kerr.	*Solanum melongena*	Leaves	Oct.	Ibadan, adults
BOSTRYCHIDAE—				
Apate monacha, F.	*Citrus sinensis*	Stem-borer	Jan.	,, ,,
HALTICIDAE—				
Podagrica dilecta, Dalm.	*Corchorus olitorius*	Leaves	Aug.	,, ,,
	Hibiscus mutabilis	,,	Sept.	Umuahia, adults
Nisotra uniforma, Jac.	*Corchorus olitorius*	Leaves	Aug.	Ibadan, adults
	Hibiscus mutabilis	,,	Sept.	Umuahia, adults
CASSIDIDAE—				
Aspidomorpha isparetta, Boh.	*Quamoclit coccinea*	,,	Oct.	Ibadan, adults
A. chlorina, Boh.	*Gossypium barbadense*	,,	,,	,, ,,
CURCULIONIDAE—				
Apoderus fuscicornis, Oliv.	*Paullinia pinnata*	,,	Aug.	,, ,,
Temnoschoita quadripustulata, F.	*Elaeis guineënsis*	,,	,,	,, ,,
Rhynchophora phoenicis, F.	,, ,,	Shoots	Nov.	,, larvae
	DIPTERA.			
ANTHOMYIIDAE—				
Atherigona excisa, Thoms.	*Eleusine coracana*	Shoots	Sept.	Ibadan, larvae
	ORTHOPTERA.			
ACRIDIDAE—				
Catantops melanostictus, Schaum	*Nicotiana tabacum*	Leaves	July	Ilesha, adults
Stenocrobylus festivus, Karsch	*Psidium guayava*	,,	Aug.	Ibadan, adults and nymphs
	Mangifera indica	,,	,,	Ibadan, adults
Cyrtacanthacris aeruginosa unicolor, Uv.	*Aspilia latifolia*	,,	,,	,, nymphs

SHEEP SCAB: REMEDIAL MEASURES REVIEWED.

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(Plate II.)

Sheep scab has existed from early times. It was known to the ancient Greeks and Romans ; it was familiar to the Hebrews ; and writers on agriculture in the Middle Ages were acquainted with its ravages, and suggested means of preventing and curing it. Laws to control the disease were introduced in Britain at the beginning of the eleventh century, and subsequently other countries also adopted legislative measures against it. Regulations have been renewed and amended from time to time to conform with the progress made in the studies of the disease and its cause. The strictness with which they are applied vary in accordance with the economic importance of the sheep industry in any particular country, and their success as preventive measures is dependent upon their stringency and upon the co-operative support given to them by all sheep-owners.

Sheep scab is a disease which in many countries continues to cause much anxiety to the majority of flock-owners. There are, however, certain farmers who regard it as something to be accepted and suffered as chronic and incurable, and consequently to be put up with ; they practice the formality of dipping in order to conform with the law, and perhaps to ensure a fair crop of wool. It must also be stated that a vast amount of literature has been published on the various aspects of sheep-scab control and eradication, much of which is confusing to the layman, who has neither the time nor the training to enable him to search the literature. Only a small proportion of the mass of literature has been available to the writer, and from a perusal of this it appears that there are differences of opinion on policies of control, apparent discrepancies in the recommendations on treatment, and what would seem to be inconsistencies to the farmer anxious to adopt the best methods practicable under his particular conditions. Many publications dealing in general with the disease and its control omit the important details essential to the practical farmer. Not infrequently authors content themselves with repeating the advice of others without verifying or extending the observations made, and applying them to local conditions.

The scab mite lives on the skin of sheep, and may be found in the wool in cases of heavy infestation. It is usually spread from sheep to sheep by direct contact. Sometimes it may be transferred to healthy animals if they are kept in an enclosure recently occupied and contaminated by scabby sheep. There is nothing to support the old belief that the disease appears by spontaneous generation when the sheep are in poor condition ; but there is some evidence indicating that the mites on untreated sheep tend to disappear at certain periods of the year, or during some phase of the disease, only to reappear later in many cases. The difficulty experienced in finding live mites during certain periods is suggestive of a latent or relatively inactive stage in the life of the mite—a difficulty which may mislead casual inspection or deceive even the careful diagnostician. It will be shown later that there are certain sites favoured by the mites ; these should be searched when parasites appear to be absent from other parts of the body.

It is generally accepted that the mites can be destroyed, and the disease cured, by the application of parasiticides in the form of dips or baths, and dressings. It is acknowledged that proper treatment involves repeated applications within specified periods, and that the preparations used must penetrate the wool and come into contact with the parasite. The interval between any two dippings has been determined by studies on the life-cycle of the mite. It has been shown that the eggs may survive the first dipping and hatch out to form a new generation. A second treatment is therefore necessary to ensure that this new generation does not develop and deposit eggs. The principle of double-dipping within the prescribed period has been accepted as sufficient to control the disease. Theoretically this is, no doubt, sound ; from a practical point of view, a third dipping is sometimes advisable, especially where the previous dippings have been hurriedly done or when infestation is heavy and crusty layers of scabs have been left unbroken.

The legal provisions for the control of sheep scab are fundamentally similar in most countries. In Britain, it is a notifiable disease. The execution and enforcement of the regulations appertaining to affected animals are vested in the local authorities acting under the guidance of the Minister concerned. The policy of isolation of scab-infested sheep, their detention and enforced dipping is governed by law when necessary ; and inspectors are appointed to advise and assist in the control of disease. Movements of diseased sheep are restricted, and the importation of such animals regulated. The laws also help the farmer with advice on the preparation of suitable and effective dips against sheep scab ; they control proprietary sheep-dips by approving only those which, on analysis, satisfy the official chemist that they are of the recognised standard strength. A proprietary dip must be labelled with a statement that it has been approved by the Minister and giving the directions for the dilutions to be used. The law also includes clauses .on the cleansing and disinfecting of places and things used for, and which have been contaminated by, infected sheep. The rules and regulations, however, are often explained and amplified by less ambiguous advisory leaflets made available to those seeking information.

The situation with regard to scab in Britain is that outbreaks have been reduced to a comparatively small figure, though there are fluctuations. It is most prevalent in, though not always confined to, the thinly populated mountainous and moorland districts where the flocks range over wide unfenced areas, and where a complete gathering of sheep for examination and proper treatment is difficult to achieve. What may be the reluctance of Government to interfere unnecessarily with the enterprise of other industries, and the difficulties of fencing and of sheep control on the part of farmers, no doubt account for the persistence of sheep-scab in the island of Britain.

Australia and New Zealand present a different picture. The sheep industry constituted their principal economic feature, and sheep scab threatened to ruin the source of livelihood of the colonists. Legislation was introduced early in the nineteenth century ; and, apparently, the flock-owners made determined efforts to eliminate the disease. The policy was similar to that adopted in Britain ; it was more rigidly enforced in every direction and rigorously applied for many years. The States were divided into a number of districts, each of which was in charge of an inspector who was authorised to inspect, seize, detain, and if necessary, resort to the treatment of sheep at the owner's expense. Severe penalties were provided for any person obstructing the inspector or refusing to give information as to the origin of any sheep, or refusing to carry out instructions regarding disinfection of vehicles, etc., or dipping of sheep. Owners of scab-infected sheep were required to warn people of the existence of the disease, to brand diseased sheep and to prevent movement. Quarantines were enforced, and heavy penalties, including imprisonment, were imposed on persons removing sheep from those quarantines.

The methods were bold and drastic, but thoroughly effective. The history of the campaigns in both Australia and New Zealand is most interesting. In 1864, Queensland was free from scab ; in 1868 the disease had been eradicated from New South Wales ; in 1871, South Australia was clean ; in 1876 and 1879, Victoria and

Tasmania respectively were declared free; and in 1898, when the disease was eradicated from Western Australia, sheep scab was finally extirpated from all Australia. New Zealand cleaned its last infected flock about 1885; the last certificate, however, was not issued until 1890.

In the United States of America, sheep scab was formerly widely distributed; it was the greatest pest that sheep farmers had to contend with. The regulation to prevent the spread of scabies in sheep prohibits the "picking" of a flock or the removal of any visibly diseased animal and then offering any portion of the remaining flocks for inspection or movement. Vehicles of transport for diseased sheep must be prominently placarded. Segregation and quarantine are enforced, and provisions are made for compulsory dipping. An organized system of inspection and supervision is in force; and other conditions analogous to those in the English Sheep Scab Order[1] are incorporated in the regulations. Trading interests, however, are treated as subsidiary to administrative control. Considerable reduction has been effected in the incidence of the disease, which has nearly been cleared out of the greater part of the Western States. At present, it is largely a matter of cleaning up relatively small infections in the range areas of Louisiana, Arkansas, Missouri, Iowa and Minnesota, and in scattered portions of the mid-western States.

Canada appears to be in the happy position of having eradicated sheep scab. The "Regulations relating to Sheep Scab"[2] are short but comprehensive, and include the rule that no sheep or any wool or other portion or product thereof shall be removed out of any place declared to be an infected place without a licence signed by an inspector. Inspectors may order scab-infected sheep to be collected, detained, isolated, dipped or otherwise dealt with, as may to them appear advisable; and they may order that no sheep shall be allowed access to any field, common yard, stable, or other place or premises where sheep scab exists or has existed. Compensation is paid only in cases of authorised slaughter of scabby sheep.

The Union of South Africa, which has made a substantial and rapid advance among the sheep-raising countries, has made similar strides in the reduction of scab outbreaks. The total number of outbreaks for the six provinces has been reduced from 2,250 in 1926–27 to 424 in 1933–34. The heaviest infection is reported from the Cape Province, which is subject to severe drought conditions, and stock have to be moved far afield for grazing. The Orange Free State is practically free from sheep scab. In the scab regulations[3] scab means a disease in the case of sheep caused by mites known as *Sarcoptes scabiei* var. *ovis* and *Psoroptes communis* var. *ovis*, and in the case of goats by the mite known as *Sarcoptes scabiei* var. *caprae*, *Psoroptes communis* var. *caprae* and *Chorioptes* (*Symbiotes*) *communis* var. *caprae*. Areas are scheduled as native areas, isolation areas, protected areas, and semi-protected areas. Veterinary inspection, compulsory dipping, restricted movements of sheep, cleansing of premises, etc., used by infected sheep are provided for. Compensation may be paid for sheep lost as a direct result of dipping under official supervision.

Basutoland illustrates a courageous effort to cope with the disease among native-owned flocks. In 1923 it was estimated that approximately 50 per cent. of the flocks were infected with scab. In 1926 there were about 2 million sheep in the territory, a large proportion of these being Merinos, the most valuable possession of the Basutos. In spite of the altitude (7,000 to 11,000 ft.) of the best sheep country and the difficulties of transporting material for the construction of dipping tanks, a policy of compulsory simultaneous dipping reduced infection so that in 1934 no outbreaks were reported. In the "Rules for the Prevention of Scab"[4] the sarcoptic, psoroptic and symbiotic parasites of sheep and goats are included as causal organisms of the disease. Inspectors—European and Native (as dip supervisors)—are engaged in a campaign of control. Sheep may be branded according to the area of origin, and all infected sheep must be marked. Movements from one area to another are controlled. No infected flocks in tanked areas are allowed to move until they have passed through three dippings.

It is hardly necessary to outline the legislation concerning scab in all sheep-raising countries ; and it is clear that the liberty of the farmer is not interfered with so long as he deals efficiently with the disease in the course of his ordinary routine on the farm.

Diagnosis.

The detection of scab in its early stages is extremely important ; it enables the farmer to arrest its spread before extensive damage is done and reduces the amount of labour and difficulties in treatment. The absence of clinical symptoms even in the case of woolled sheep renders early detection and diagnosis difficult, and demands considerable experience and powers of observation. In well-established cases detection is comparatively easy, except, perhaps, in the fine-woolled breeds, in which the mites lurk in the heavy folds. In non-woolled sheep lesions are not easily discernible, and such animals may maintain and spread infection.

Frequent and regular inspection of flocks is essential therefore ; and if any animals show symptoms of the disease, a closer examination may reveal live parasites. Then treatment of all sheep which have been, or are suspected to have been, in contact with that animal or flock should be resorted to without delay.

Farmers with large flocks and good shepherds look upon scab as a serious menace, and deal with it accordingly ; but those with small flocks (possibly a dozen or more to provide meat for the table) are apt to ignore the existence of the disease among their sheep, or consider it as trifling, and neglect treatment. There are some, also, possessing large and numerous flocks who do not insist on periodic inspection of the sheep ; or when the flocks are gathered for this purpose regard the straying of a few sheep as unimportant, not realising that those stray sheep may harbour the parasite and form a nucleus for re-infection of the flock.

It is obvious that no reasonable system of official inspection can be as effective in locating infective sources as the diligence of the farmer himself, on whom falls the onus of early diagnosis. In this connection the policy of table inspection adopted in the Basutoland campaign of eradication is noteworthy. In order to determine whether a flock is clean or otherwise, every sheep is caught and placed upon a table for thorough examination.

Hand-dressing.

The complete immersion of sheep in a dipping fluid is the customary remedy for scab. In chronic cases, however, layers of hard crusts or scabs prevent the penetration of the liquid to the mites which are often secreted beneath. These scabs must be broken up with a light curry-comb or an old maize cob, and hand-dressed prior to dipping. The hindquarters may be fouled with faeces, which should be removed. There are other sites favoured by the mites which demand careful attention and treatment ; they are the inside of the ear, the lachrymal or infra-orbital pouches—the pits or cavities below the eyes ; the bases of the horns, the perineum, the prepuce of the rams, and the wrinkled scrotum of the castrated male or wether.

Compounds recommended as hand-dressings include a mixture of fuel oil and sulphur ; two parts of Stockholm tar, two parts of oil, and one part of turpentine ; a mixture of two parts of linseed oil and one part of paraffin ; solutions of the dipping fluid at normal or double strength of the bath dilution ; and in some instances tobacco extract in oily or greasy media.

As dipping in an aqueous solution is usually carried out soon after hand-dressing, it is better to confine the use of oily mixtures to the ear cavities and the lachrymal pouches, as these mixtures tend to hinder the uniform penetration of the dip through the fleece. A short, stiff-bristled brush is useful for cleaning the glandular lachrymal pouches, and a slightly longer brush is convenient for dressing the deeper cavities of the ears.

Hand-dressing the visibly affected lesions is not in itself effective as a cure. The South African regulations provide for the prohibition of the hand-dressing of sheep in lieu of dipping. An American bulletin[5] on sheep scab states that hand-dressing or " spot-doctoring " acts as a palliative and tends temporarily to check the disease, but will not cure scab. It adds that in many cases it is responsible for spreading the disease, for the reason that the sheepman too often depends on this method to effect a cure.

It should not be necessary to point out that the use of a poisonous solution or mixture in hand-dressing should be followed by careful washing of the hands, especially where natives are employed ; and that in using lime-sulphur dressings the hands should be well smeared with oil or grease to avoid severe blistering of the skin.

Counting and Marking.

There is no doubt that the counting of sheep at a gathering of the flocks has many advantages ; it acts as a check on the number in the stockbook or register, and is a means of accounting for any losses from death or straying. The shepherd may be able to make a further search for stray sheep, and to ensure that no animal is omitted from the treatment to be given in the case of an outbreak of sheep scab. Strange sheep may be present and by enquiry their origin may be ascertained ; and it may be possible to trace the source of infection.

When hand-dressing is being carried out, comparatively little additional labour is involved in marking those which have been examined and treated ; and this enables the farmer to identify at a glance any animal which may have joined the flocks after hand-dressing, or which may have escaped attention.

It is needless to emphasize that unmarked sheep in the flock should receive treatment whether they belong to the farmer or not.

Dipping Tanks or Vats.

There are several types of dipping tanks, vats or baths, in common use ; they vary in size, form and construction according to the requirements and taste of the owner. When there is only a small number of sheep to be dipped, a portable canvas bag may be used. A sheep may be lifted into this, and held in the liquid for the required length of time, and then taken out to the draining floor. It is a laborious and troublesome method, however, and suitable only when six or a dozen sheep exist on the farm.

The simple galvanized iron portable tank is convenient for a flock of a few hundred sheep. Each sheep must be handled and raised into this tank ; but it is possible to treat many sheep in a day by this method. It has advantages in that it requires little fluid, and the cost is low. The drawbacks are the amount of labour involved in immersing the sheep and the need of holding them for the full period of immersion. In some cases the animals have to be turned on the back and held in the dip—care being taken that the head is held above the surface. The restlessness and splashing of the sheep is not pleasant ; and in some cases dangerous to the operator and to the sheep.

The cage bath appears to be less popular. It consists of a galvanized tank sunk in the ground. In this, a cage is raised and lowered by a windlass. One sheep at a time walks into the cage, and is lowered into the bath. In due course, it is raised, and the sheep passes on to the draining yard. Handling is reduced by this method, labour is made easier, and risks are reduced to a minimum.

For large flocks, and where dipping is practised as a routine, it is necessary to provide permanent tanks. The initial cost is greater but is compensated by the saving in labour, and the efficiency in dipping large numbers of sheep. These large tanks may be constructed in stone and concrete, or in wood. Obviously the former is the more permanent. There are two types—the straight-run swimming tank and the circular (with or without a central island). Both of these permit the sheep to swim in the dipping solution ; and continual movement assists penetration of the dip and the thorough soaking of the fleece.

The circular tank seems to have certain advantages over the straight-run tank. In the latter it is often difficult to avoid crushing at the outlet ; the animals have to be turned-over frequently and kept moving. When turning there is a tendency for the hooves of one or other of the legs to cut or graze the other and cause bleeding and possibly poisoning. Drowning sometimes occurs when too many sheep are put in at a time ; and injuries are not infrequently caused by rough-handling. The straight-run type requires a larger number of attendants than the circular, the use of which reduces labour and difficulties of handling to a minimum. With the circular dip the sheep are allowed to swim more freely and do not become fatigued by rough handling.

It has been estimated that in order to allow a sheep to swim for two minutes in a straight-run tank without turning, the tank should be about forty yards long ; in a circular tank, it is merely a question of going round repeatedly until the time is up.

Permanent dipping tanks deteriorate if not given proper attention when not in use. They should be kept full of water to avoid cracking, and before dipping operations it would be well to test for leaks and overhaul if necessary. The pressure of the ground against the sides of an empty tank tends to cause them to bulge inwards ; and when these sides are of cement or concrete they crack very badly.

Dips and Dipping.

The active ingredients which are most commonly employed in the manufacture of dips are arsenic, tar acids, sulphur, tobacco or nicotine. Sulphur may be mixed with arsenic or calcic compounds, tobacco or caustic soda. In practically all countries provision is made for the guidance of the farmer with regard to the proper strength and percentage of the active ingredients in all products for dipping against scab, and prescriptions are given to enable the farmer to prepare his own dip when he so requires.

In Britain lime-sulphur dips must contain no less than 1 per cent. sulphur sulphide, which may be obtained by using not less than 18 lb. sulphur with 9 lb. good lime for 100 gallons. The Australian prescription for lime-sulphur is equivalent to about 33 lb. sulphur and 11 lb. lime to every 100 gallons of dip ; the New Zealand mixtures consists of 25 lb. sulphur and 12½ lb. lime to a 100 gallons of water ; the American regulations[6] stipulate that a lime-sulphur bath must at all times be maintained at a strength of not less than 1½ per cent. of sulphur sulphide, and the preparation should be made up of 24 lb. flowers of sulphur or sulphur flour, 8 lb. unslaked (or 11 lb. commercial hydrated, not air-slaked) lime to 100 gallons of water. In South Africa approved lime-sulphur is prepared from 25 lb. sulphur mixed with 15 lb. unslaked lime (or 20 lb. slaked lime) to every 100 gallons of fluid. This, along with commercial lime-sulphur or soda-sulphur concentrates sold under directions, must contain when diluted for tank use a strength corresponding to not less than 1·5 per cent. sulphur sulphide.

According to regulations in Britain, nicotine dips must contain not less than 0·1 per cent. nicotine ; in America and South Africa a dip strength of not less than 0·05 per cent. of nicotine must be maintained.

Tobacco, nicotine or nicotine and sulphur dips may be prepared in several ways. The proportions and instructions in the preparations of these in different countries are :—

England.

Tobacco and sulphur.—Steep 35 lb. of finely-ground tobacco (offal tobacco) in 21 gallons of water for four days. Strain off liquid, and remove the last portions of the extract by pressing the residual tobacco. Mix the whole extract, and to it add 10 lb. of flowers of sulphur. Stir the mixture well to secure an even admixture, and make up the total bulk to 100 gallons with water.

Australia.

Tobacco and sulphur.—Infuse good leaf tobacco in 100 gallons of water which has been brought to the boil. Cover the utensil used to prevent the escape of steam which might carry off with it some of the active, curative properties of the tobacco; draw off the infusion and add fresh water to the tobacco until extraction is complete. The amount of tobacco used should be less than 20 lb. to 100 gallons of water. To the liquid extracted add, and mix thoroughly, 20 lb. of sulphur.

America.

Nicotine and sulphur.—The formula for this dip is given as four-tenths of a pound of nicotine, 16 lb. flowers of sulphur, 96 gallons of water. This mixture contains not less than 0·05 per cent. nicotine and 2 per cent. sulphur. In this case 1 lb. of a 40 per cent. solution of nicotine would suffice for 96 gallons of water.

There appears to be no formula for a home-made tobacco or nicotine dip recommended in South African publications on sheep scab and its treatment. Tobacco and sulphur dips were used for scab control in New Zealand and were apparently successful.

A prescription containing carbolic acid and soft soap is officially approved by the Ministry of Agriculture and Fisheries in England. It may be prepared by dissolving 5 lb. of good soft soap, with gentle warming, in 3 quarts of liquid carbolic acid (containing not less than 97 per cent. of real tar acid). Mix the liquid with enough water to make 100 gallons.

A tar dip must contain not less than 0·76 per cent. of total tar products, of which not less than 0·36 per cent. shall be tar acids.

A caustic soda and sulphur dip may be made by mixing 20 lb. of sulphur into a thin cream with not more than 2½ gallons of hot water and sprinkle into this 5 lb. of caustic soda with constant stirring. After 40 minutes the resulting mixture is poured into 100 gallons of water for tank use.

With regard to home-made lime sulphur dip it is agreed that the lime should be thoroughly slaked and free from hard lumps. The finely powdered lime should be mixed with the appropriate portion of finely ground sulphur or " flowers of sulphur " to make a thick, homogeneous paste with three or four gallons of water. The paste is then transferred to a vessel containing boiling water and boiled for a time. The prescription given in the leaflet issued by the Ministry of Agriculture and Fisheries recommends placing the mixture or paste in a strong cloth, tying the ends and suspending in a boiler containing 10 gallons of water so that the water completely covers the contents of the cloth. The cloth must not touch the sides or bottom of the boiler, as otherwise the cloth may be burnt and its contents escape. The boiling should continue for two hours, when the cloth should be removed, taking care that none of its contents escape into the water. The solids can then be thrown away. The liquor in the boiling utensil should now be made up to 10 gallons with additional water, and poured into a tight drum or barrel. This quantity is sufficient when mixed with water to make a 100 gallons of dip.

According to the South African recommendation, the well-mixed paste is thrown into a pot containing 25 to 30 gallons of boiling water and boiled for 30 to 40 minutes. The contents of the boiling-pot are transferred to a barrel, and after allowing the sediment to settle the clear fluid is run off into a dipping tank from a bunghole four inches from the bottom of the barrel. One hundred gallons of water are then added to bring to tank strength.

The quantity of water used with the paste for boiling is of importance, in so far that a small quantity of water affects the solution of lime, and the proportion of sediment, when the paste is not contained in a bag or cloth, is proportionately greater. If the paste is not covered, the boiling mixture can frequently be stirred to prevent the paste from settling and caking on the bottom of the vessel, and to assist the combination of the ingredients. When the mixture can be stirred in this manner, it would appear unnecessary to boil for more than forty minutes ; but if it is held in a bag the period of boiling must be extended to two hours. It is interesting to note, however, that the American Bulletin recommends boiling the loose paste in thirty gallons of water for two hours, frequently stirring the mixture.

The final liquor should be of a chocolate or dark-amber colour and should not contain any sediment, as this will injure the wool and the eyes of sheep.

Special mining and sedimenting tanks can be constructed for dip-making ; or the farmer may choose one or other of the more simple methods quoted above.

The home manufacture of tobacco and sulphur dip seems to be a lengthy and tedious process, hardly practicable to the ordinary farmer. The nicotine and sulphur dip is a more convenient mixture. The nicotine solution and the sulphur should be mixed together with water before adding them to the water in the dipping tank ; and it will be borne in mind that the dip should be heated.

These are the usual home-made dips ; and many more proprietary makes are available to the farmer. There has been some controversy as to the relative values and efficiency of the home-made brands and proprietary products. It is not proposed to enter into this dispute. It will suffice to state that there is, for the farmer, a wide range of choice from home-made and proprietary dips which have proved effective in destroying the scab parasite. The cost of a dip will naturally affect the farmer's choice, but while it requires consideration there are other matters also to be taken into account. A product when diluted according to instructions should prove destructive to the parasite ; it should also serve as a protection against re-infection to some extent, and to kill the larvae which might emerge from the eggs. With reasonable and proper care in its preparation and use, the dip should be safe to the labourers and to the sheep. The solubility of the concentrate is an important factor, as is also its penetrative qualities. It is obviously more desirable from a practical point of view that a dip be effective when used in a normal cold solution. Heating apparatus increases the costs of dipping operations. The dip should not discolour or affect the value of the wool. The portability of the concentrate or of the ingredients needs consideration where transport is difficult or costly. The question of labour, especially with home-made products, must be taken into account in estimating the costs involved. The quality of the ingredients must also receive attention as will be seen later in this article.

Experiments carried on under the direction of the Sheep-Dipping Committee in England in 1904[7] demonstrated that lime-sulphur, arsenic and sulphur, carbolic dips, tobacco and sulphur, and others, were quite effective against the scab-parasite, and did not deteriorate the quality of the wool further than to discolour it to some extent. Since that period the preparation of dips has improved ; the amount and proportion of ingredients in concentrates have been adjusted, and dilutions carefully studied and established so that, consonant with scab-curing properties, their injurious effect is practically negligible when administered properly.

In a pamphlet[8] on Sheep Scab issued by the British Ministry of Agriculture and Fisheries, prescriptions for three home-made dips are given ; and it is explained that the Ministry has not included in their Schedule any preparation containing arsenic. " It is not to be assumed, however, from this omission that the Ministry does not concur in the view that arsenical dips are thoroughly effective against sheep scab. There is a possible danger to human beings, attendant upon the preparation of such dips, which renders it advisable that the dips should be compounded by qualified persons only. It is also important to note that a certain amount of risk may be incurred by dipping sheep twice, with a short interval, in a poisonous dip, and that when a poisonous dip is used for the first dipping, it is much safer that a non-poisonous preparation should be used for the second." The prohibition of the use, for the second dipping, of a dip containing arsenic in the Sheep Scab Order of 1928 was revoked in the Sheep Scab (Amendment) Order of 1928 (4634)[9], and it appears that owing to pressure by the National Farmers' Union, the Ministry has recently waived its prohibitions of arsenic on the understanding that no liability be incurred unless the instructions on the labels of sheep dip containers are strictly followed. In addition, the Ministry recommends that for the second dipping, half the prescribed strength be used, and it accepts this practice as conforming to the Order.

In Basutoland, a proprietary brand of arsenical and sulphur dip was used at full strength instead of half-strength for the second dipping. No untoward effects were experienced, and it was stated[10] that " in practice where one employs a native staff this is an advantage, though of course it is not so cheap."

Arsenic, nicotine and cresol dips are used against sheep scab on the continent of Europe, the first being generally used in France, and the last most popular, apparently, in Germany. The use of arsenic dips is sometimes followed by poisoning, especially if the skin suffers injury during shearing ; it is for this reason that they were displaced in some countries by other dips. In Prussia several cases of poisoning were observed as a result of dipping sheep in creolin dips ; and it is stated in the American bulletin[5] on " Sheep Scab " that " it is dangerous to dip sheep in some of the dipping preparations, especially lime-and-sulphur, if there are any fresh wounds on the animal." In America, it is the opinion of the authorities that the dangers inherent in arsenical dips should restrict their use to fields where, as in the eradication of cattle ticks, no safer dip is practicable.

In South Africa " losses have occasionally been encountered, especially in sheep and goats, after dipping in the so-called ' phenolic ' or ' tar-product ' dips."[11] On the other hand, the present satisfactory situation with regard to sheep scab in Basutoland is largely, if not entirely, due to a proprietary brand of arsenic and sulphur dip.

In England, dipping products are officially approved on the basis of chemical analysis, the number of approved dips being approximately 300[12] ; the chemical works of nearly all provincial towns appear to produce dips. In the United States of America, dips permitted for use in official dippings are restricted to specific compounds of lime-and-sulphur and nicotine mixtures. Proprietary brands of both types may be used in official dipping only after specific permission has been issued by the Bureau. The regulations state that " No dip other than the lime-and-sulphur or the nicotine dip will hereafter be given department permission for use in official dipping of sheep for scabies, unless it has been shown to the satisfaction of the Bureau (1) that the strength of the bath prepared therefrom may be satisfactorily determined in the field by a practical, portable testing outfit ; (2) that under actual field conditions the dipping of sheep in a bath of definite strength will effectually eradicate scabies infection without injury to the animals dipped."

In South Africa, the approved dips which have been sanctioned for the dipping of infected sheep under official supervision comprise home-made and certain registered proprietary brands of lime-sulphur which give a tank strength of 1·5 per cent. sulphide sulphur ; tobacco extracts and nicotine products (which when diluted contain not less than 0·05 per cent. nicotine)—about 5 in number ; two (with a third recently registered) powdered forms of arsenic-sulphur dips ; three phenolic and tar distillate dips ; and two containing other active ingredients.[11]

The protection afforded against scab-infection by certain dips is shown in the experiments carried out by Bedford in South Africa (1915).[13] A diagram illustrating his results shows that lime-and-sulphur gave protection for just less than 5 days; some brands of tobacco dips protected the sheep for a shorter period, while one was effective for a little over 5 days; another dip containing other ingredients prevented re-infection for about 11 days; and two arsenic-sulphur dips provided protection for about 14 and 16 days respectively.

To quote an American authority[5] " The dip that is left in the wool after dipping will often serve, for a limited period of time, as a preventive against re-infection. The length of this period of protection varies with the climatic conditions and the kind of dip used. If sheep are exposed to frequent, heavy rains after dipping, much of the dip will be washed out of the fleece. A dip containing sulphur acts as the best preventive against re-infection. Under average conditions such a dip will probably afford protection for a period of from 30 to 60 days and, under favourable conditions, for a much longer time."

According to Verney,[10] Green & Bedford report most favourably on nearly all the dips on the market, but as a prophylactic the arsenical dips appear to be the best.

In preparing the concentrate of a home-made type of dip it is not sufficient to guess the weight of the ingredients or the measure of liquid. All must be done with accuracy and care. It would be reasonable to ask—say in the case of lime-sulphur—which of the formulae quoted above should be adopted for dipping purposes. The proportions used in the English and New Zealand prescriptions is 1 of lime and 2 of sulphur; in the Australian[14] and American dips the proportions are 1 of lime to 3 of sulphur; and in South Africa 3 parts of unslaked lime are used with 5 parts of sulphur. The quantities of both ingredients also differ. The farmer might easily become confused with these differences. It may be explained, however, that the composition of the dip depends upon the quality of the lime obtainable and its combination with the sulphur to form the necessary sulphide (or polysulphide) compound. The sulphur also must be of good quality and used for mixing in the form of a very finely ground powder or flour.

The equation of the chemical reaction of lime and sulphur is approximately a ratio of 1 part of lime to 2·29 of sulphur, but in practice the combining ratio is slightly lower—about 1 : 2·11. It is not proposed to enlarge on this aspect of lime-sulphur preparation beyond stating that researches[15] into the chemistry of dips and the quality of local limes (when recommending lime-sulphur) is of economic and practical importance. Studies along these lines have been pursued in South Africa; but apparently they have not been completed.

Green,[15] working in South Africa, states that in general practice it is highly important that the lime used be of a high grade. Although it has been shown that a dip much below the concentration obtained from a high quality lime is still effective in curing scab, the use of a low quality lime is uneconomical and liable to give uncertain results. The lime used in the manufacture of lime-sulphur dip should be of better quality than that utilised for ordinary liming of the land and should contain a high percentage of calcium oxide.

Failure to adhere to the directions in preparing the concentrate or the diluted dip may account for injuries to the sheep and discoloration of the wool. There have been several tests and experiments on the effects of different dips on the quality of the wool. They indicated that when carefully prepared and properly used the majority have little or no significant injurious effect. It is reasonable to suppose that dipping soon after shearing tends to affect the wool to a less extent than dipping when the wool is long and ready for shearing.

The experiment carried out on the influence of regular dipping on the merino sheep and its fleece at the Bathurst Experiment Farm in South Africa[16] is of particular interest. One lot of 30 sheep was dipped weekly for twelve months in arsenite of soda of a strength of 2 lb. to 100 gallons of water ; a second lot of 30 was similarly dipped in water ; and a third lot used as control. The results showed that weekly dipping did not influence the condition of the sheep as reflected in body weight ; all sheep dipped in arsenite of soda survived after a year's treatment, and were always free from ticks and blowfly trouble ; arsenite of soda had no influence on fleece weights, fibre thickness, staple length or fibre contour. As regards colour, handle and appearance, the wools dipped in arsenite and in water deteriorated to some extent. Deterioration was practically of the same degree in the two dipped groups, and presumably due to the hardness of the Bathurst water and not to the arsenite of soda dip. As regards monetary value there was as much as 1d. a pound difference between the noil from the control and that from the dipped lots ; and in the top a difference of 2d. a pound.

The frequency of dipping sheep as an anti-scab measure is dependent upon the existence and persistence of the disease. It may be taken that when the disease is diagnosed among the flock treatment should immediately follow. It is usual, however, for the farmer to consider the crop of wool and, if shearing time is near, to hand-dress any badly infested sheep and await the completion of shearing before resorting to dipping.

The recommended interval between the completion of shearing and the dipping of sheep varies. Some authorities state that the sheep should have sufficient wool to carry away enough dip for future protection. Merinos should be dipped not less than four to six weeks after shearing, and long wools eight weeks after being shorn. Others maintain that sheep should not be dipped immediately after shearing, but that a period of at least ten days should elapse between shearing and dipping, in order that the shear cuts may heal. In early text-books, it was advised to dip three or four days after shearing. As a basic principle it may be accepted that short wool permits the dipping solution to penetrate to the skin—and the parasites—more quickly and uniformly ; long wool, especially if thick and abnormally rich in yolk, may prevent the penetration of the dipping fluid or cause it to be unevenly distributed. On the other hand, the longer the fleece the longer may the dip deposit be stored on the sheep, and possibly exert its effect for a longer period.

In preparing the bath and estimating the amount of material, and the quantity of liquid which may be required for dipping, it is advisable to ascertain the capacity of the tank, and to allow for the amount of fluid which will be carried out in the fleece of the sheep. Sheep in full fleece will retain more of the dip in the wool than freshly shorn sheep, and short-woolled lambs will carry out, on an average, from one to two quarts of dip depending on the size of the sheep and the length and nature of the wool. An average-sized sheep with medium wool will take out about a gallon of dip, whereas a full-fleeced, fine-woolled sheep may retain in the fleece nearly two gallons. Wilken-Jordan and others[17] state that the average quantity of dip lost is about 0·59 gallons per animal ; the minimum and maximum limits being 0·23 and 1·19 gallons respectively. Where there is no roof to the dipping tank an allowance should be made for evaporation if dipping occupies several days.

In some countries the lime-sulphur and tobacco or nicotine mixtures are used as warm dips. In the American bulletin, to which reference has already been made, it is stated, " The temperature of the dip should not be a matter of guesswork, but should be ascertained accurately by using a thermometer. If it is too high the sheep may be injured, and if too low, failure to cure will probably result. In field operations, when dipping is supervised by inspectors, the temperature of the dip is maintained at 100 to 105°F. Practices demonstrated that the lime-and-sulphur and nicotine dips should be used at these temperatures. The coal-tar-creosote and cresylic-acid dips should be used at slightly lower temperatures, the maximum for these being 95°F."

In Australia (New South Wales), Bruce[14] recommended that when the fleece is short, the bath (tobacco and sulphur) should be administered at a temperature of 115°F. in winter, and at 110°F. in summer, at which it should be the endeavour to keep it throughout the dipping (the thermometer being tried every other dipful) ; and the sheep should be allowed to remain in the dip from 60 to 80 seconds, and as much longer as they can stand it ; for with short fleeces they dry almost immediately after being put into the draining yards, and if the bath was not severe both as to temperature and duration, they would stand less chance of being cured than if they were in full fleece or nearly so, whereby they take out and retain more mixture. As the mixture cools it will be necessary to keep the sheep longer in it, say from 1½ to 2 minutes altogether, but in no case should the temperature be allowed to fall below 105°F. When the fleece is long, the same writer stated, the heat of the mixture should be maintained at from 105 to 110°F. The use of lime-sulphur mixture should be similar to that of the tobacco and sulphur. In a footnote, it is further explained that while it takes only 30 seconds to kill the scab mite with the mixture at 90°F., it will live for 10 or 12 minutes in the same mixture at 45 or 50°F.* and that a high temperature will doubtless kill many of the eggs of the acarus. Hutyra and Merek[18] remarked that cresol dips were used at a temperature of 96 to 100°F., and that the sheep were held in this bath for three minutes.

It is somewhat significant that lime-sulphur dip especially has been utilised successfully against scab at a comparatively low temperature, and thus without additional labour and expenditure on accessories for heating and maintaining a relatively high temperature.

While there may be advantages in using a warm dip, it does not seem to include a considerable reduction in the period for which the sheep are kept in the bath, for in the United States of America it is recommended that " the time that infected sheep are held in the bath should in no case be less than 2 minutes ; if the scab is not advanced, from 2 to 3 minutes in the vat is sufficient. But in well-advanced cases of hard scab on fine-wool sheep, especially bucks, better results are obtained if they are held in the vat from 3 to 5 minutes during the first dipping. If the hard scabs and crusts are broken up and soaked with dip before the sheep are dipped, it is not necessary to hold them in the vat longer than 2 minutes." A warm dip would, of course, penetrate the fleece better, and no doubt it would more readily soften hard scabs and kill the parasites.

Having touched upon the period sheep should be kept in the dipping fluid, the apparent discrepancies in recommendations may briefly be discussed.

In the Sheep-Scab Order of 1928 " dipped " and " dipping " mean a thorough immersion in the dipping-bath of the whole sheep (including the head and ears), and keeping the sheep (excluding the head and ears) in the dipping-bath for not less than one minute. In Leaflet No. 61, where prescriptions are given for the preparation of three home-made dips, there is included a note " The period of immersion in these dips should not be less than half-a-minute." The opinions expressed in the American bulletin are quoted above. It will be seen that sheep can often withstand much longer periods of immersion than one minute. Sheep in poor condition, of course, cannot tolerate such a long period as those in good health. In South Africa, as in Basutoland, the period of immersion is stipulated as being not less than two minutes.

As the interval between any two dippings is established in accordance with the period taken by the scab-mite to complete its life-cycle, it would appear that unless the development of the mite varies, in time, with the seasons in any particular country, or the peculiar climatic conditions in different countries, there should be unanimity in the recommendations as to the most suitable and effective interval. Yet this is not so. In Britain, the second dipping should be carried out " not earlier than the eighth day, and not later than the fourteenth day after the last dipping." In Australia, the recommended interval was from ten to sixteen days ; and in New Zealand and America ten to fourteen days. The regulations in the Union of South Africa provide that the second dipping shall in every case take place within not less than eight nor more than ten days after the date of the first dipping. Bedford[13] in South Africa advises that the second dipping should always be given nine or ten days after the first. In Basutoland, it is customary to hand-dress and dip twice at an interval of nine days, non-infected flocks being dealt with also at ten-day intervals.

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* Temperature of dip at Naivasha.

While all these different intervals may be accepted as effective in the countries to which they apply, it would seem that a more precise recommendation, based on the minimum number of days for the completion of the life-cycle of the mite, would be more effective in practical eradication of the disease. A reasonable latitude provides for inclement weather, or other pressing duties on the farm which may disturb the normal interval of dipping ; and it may allow for delayed hatching of the acarine eggs under adverse conditions ; but these differences do indicate the need for further research into the biology of the scab parasite under various conditions, and in different countries.

Preparation of Sheep for Dipping.

When arrangements have been made with regard to the material for the dip, and for the procedure of dipping, the flocks to be treated on the appointed day should be gathered together near the tank several hours before the actual dipping. If they are allowed access to water and food three or four hours before immersion in the dip, they will probably be in the best condition for the operation. They should not be too full of food and water, however. On no occasion should the flocks be driven hurriedly from the pastures to the dip without providing water for them and sufficient rest to permit cooling off. By looking-over the sheep, and preferably by re-counting, it is easy to detect any animal which may not have been marked, or which may have joined those previously hand-dressed.

It is advisable that the rams should be dipped separately ; and as they succumb more readily than ewes or hoggets, it is necessary to give them careful attention. Frequently the rams are put into the dip before the other sheep. In such cases, the bath dilution should not be too freshly mixed, and it is important to stir the dip frequently. Verney[19] in Basutoland states that in his campaign " no sheep are allowed into the tank until fifteen minutes have elapsed after well mixing the dip in the tank." He also observes " that goats stand dipping better than sheep, and if there are goats with the sheep (a common condition in this territory), then the goats are put into the tank before the sheep."

Because of the large horns and the size of the body, rams should be allowed plenty of swimming space ; and in addition to immersing completely two or three times, the head, ears and horns should receive special treatment by ladling-up the dip in a bucket or tin and pouring over the head to ensure a thorough soaking of the wool around the horns and ears.

Particular care should be exercised in handling the sheep when they are put into the dip, and while they are in the bath. Overcrowding should be avoided, and the number of sheep in the bath at a time should allow sufficient room for movement without crushing. The attendants should see that the animals are properly arranged, and prevent them from climbing or raising themselves out of the bath at the sides or ends of the tank. Native labourers habitually take periodic rests, and hold a sheep, with a crook, so that its head and shoulders are well above the surface of the dip for a considerable time. It is essential that at every stage of the operation close supervision by a capable and reliable person be provided.

Ewes and lambs should not be dipped together. The former can usually withstand dipping better than rams, hoggets or lambs ; and it is surprising how much even young lambs can tolerate when dipped separately and permitted plenty of room for swimming. Sheep in weak and poor condition—those scouring, and infested with internal parasites—should receive special attention. They should always be assisted through the dip, or segregated for special treatment prior to dipping. On no account should they be returned to the flocks without first having been dipped.

Draining and after-dipping Treatment.

When the sheep emerge from the dipping tank, a quantity of dip taken out in the fleece drains away fairly quickly. It is desirable that this should be saved and returned to the tank. The draining pens should be constructed to allow all the surplus amount to flow back to the tank. Dirt and excreta will also be carried in the drainage, so provision should be made to collect all solid material in a sedimenting pit. Excreta and dirt will find a way—by the exit—to the dip which necessitates a periodic skimming of the dip. The cleanliness of the bath and of the sheep will depend to some extent on the state and arrangement of the pens around the tank. The draining pen, in particular, should be a bare yard (preferably with a cement floor) and with no grazing or food which may become contaminated and thus provide a source of poisoning.

After the sheep have been dipped, they should be allowed to rest and dry in the shade for not less than two hours. The lambs should be kept apart and not allowed to suckle their mothers until the ewes have dried. Rams also should be kept separate until drying is complete. If the sheep are driven quickly, and far, immediately after dipping and when wet, they may suffer from chill. Mortality after dipping is not infrequently due to hurrying the sheep back to the pastures.

A further check of the number of sheep dipped, and an examination of the state of the animals after dipping, should be carried out. This procedure involves little extra labour and trouble, but gives the satisfaction that the work has been done thoroughly ; and arrangements can be made for nursing those animals which may have suffered during the immersion, and thus reduce losses. It is well to extend the observations on dipped sheep for several days to estimate the effect of dipping, and periodic inspection should be carried out for several months to ascertain whether the disease is reappearing.

Effects of Dipping.

A sudden or drastic change in the treatment of sheep may be expected to cause some constitutional set-back, especially if any of the animals are suffering from poverty or sickness. Dipping in water alone may result in the further weakening of sheep in poor condition, and may cause mortality through chill or exhaustion. When sheep are properly immersed in a reliable dip, practically no losses or damage follow—at most comparatively little, though ignorance and negligence are often responsible for heavy losses. There is no doubt that a brand of dip is sometimes blamed for deaths when the real cause may be more correctly ascribed to faulty procedure. Deaths after dipping are not necessarily due to the composition of the dip. Reference has already been made to the experiments at Bathurst on the frequent and regular dipping of sheep in arsenite of soda, when it was shown that such dipping did not affect the constitution of the sheep as reflected in body-weight, etc. Arsenical poisoning may result from the absorption of an arsenic dipping fluid through broken skin. Sheep dipped in an overheated condition may suffer from scalding, and then absorb the arsenic through the inflamed skin. Similar trouble may arise from the use of a dip made stronger than that recommended. Poisoning may also follow the dipping of sheep with fresh wounds in a lime-sulphur dip. This is a form of blood-poisoning, apparently caused by micro-organisms entering the open wounds and the sealing action of the dip excluding the air and stopping natural drainage.[5]

It is not uncommon for sheep which have been driven hurriedly to the dip to arrive in a thirsty condition, and when they enter the dip, they swallow some of the liquid. Or the animals may receive hasty and rough treatment in the bath, and in the midst of the turmoil take in an overdose of dip. Poisoning may result from eating food or tufts of grass in the draining-pen, and from several other minor causes. Suffocation or nicotine poisoning may occur by the use of too strong and too hot a dip containing nicotine.

As to the effect of dips on wool, it may be accepted that the sooner dipping is carried out after shearing, the less effect the dip is likely to have upon the wool. Unnecessarily high polysulphide concentrations in a lime-sulphur dip would naturally involve risk of damage to the wool and probably render it less amenable to scouring and cleaning processes in general. Under normal conditions, damage to the fibre soundness of the wool is due rather to the process of dipping than to the ingredients used in the dip. The results of the most recent experiments in South Africa indicate that arsenates and arsenites tend to protect the fibre rather than to cause damage, as the yellow film staining the fibres impedes the penetration of the destructive ultra-violet rays of the sun.[15]

Records of casualties during and after immersion in an arsenical dip in Basutoland show "that 75 per cent. of the losses occurred at the second dipping, and amongst sheep that were put into the tank first after mixing a fresh tank-full of dip."[19] This suggested that the dip had not been properly mixed, and we are now very careful to train our native dipping supervisors in this direction. In addition to thoroughly mixing the powder into a thin paste in a bucket, all this has to be passed through a grain bag, and no sheep are allowed into the tank until fifteen minutes have elapsed after well mixing the dip in the tank.

In an experiment in Kenya with a dip prepared from an arsenic compound and one prepared from lime-and-sulphur mixture, it was observed that mortality was greatest after the second dipping, and least after the third dipping. The percentages of casualties after the first, second and third were 0·66, 0·75, 0·09, respectively. In each case the dip was prepared most carefully on the evening previous to the day of dipping. The results indicated that the first dipping adversely affected the weakest animals ; and the second dipping took a toll of those sheep not in so poor a condition as the first lot, but which could not withstand two immersions at a short interval. Some old native sheep soon collapsed in the lime-sulphur mixture, but recovered after a short rest.

Kraals, Bomas and new Pastures.

It was held by early writers, and believed by farmers until recently, that the scab-mite or its viable egg was able to exist for some considerable time apart from the host ; and that mites and their eggs in tags of wool torn off the sheep by wire, left on rubbing-stones, fences, gates, etc., accounted for the reinfestation of dipped sheep. It was particularly stated that the mites retained their vitality on cast-off scabs in moist places, under manure in a yard or field, or other places which afforded shelter and moisture. The stated period of vitality, under these conditions, varied from one or two months to as long as a year. Ranges or pasture-lands near watering-places exposed to sunlight were believed not to remain infectious longer than thirty to sixty days.

The experiments carried out in South Africa by Shilston[20] and Bedford & Du Toit give valuable, exact information on this point, and finally explode the old vague theories. Du Toit[21] states that his experiments with infected sheep and kraals have shown that the possibility of scab infection originating in a kraal is very small indeed. One experiment proved that if a grossly infected kraal be left empty for seventeen days, clean sheep can be put into it with perfect safety ; and another experiment showed that even this period is unnecessary *provided that the sheep have been dipped properly.*

Although Du Toit concludes that a thorough dipping is the only thing necessary for the complete eradication of scab from a flock and that it is not necessary to worry about the infection of a kraal, it seems not to be a troublesome precaution to treat moveable night bomas which may be utilised to pen the sheep immediately after dipping, especially if measures have not been taken to ensure that no strange or undipped sheep has joined the flock. These night bomas usually consist of a length of netting-wire supported by long, narrow poles ; they are easily pulled up and rolled ; they can be carried to the dip and left in the bath for a few hours before being used on a new site.

Disposal of the Dip.

After completing the dipping operations, it is customary to dispose of the liquid by transferring it to a deep pit in the vicinity of the tank. In some countries, the authorities have thought it necessary to advise farmers not to dispose of it in such a way that it may pollute rivers, or streams or other water-supplies. Amongst civilised people, it may not be necessary to remark that the sediment left in the tank is impregnated with arsenic, and the " dumping " of this mud on the surface in a place accessible to any stock is liable to cause poisoning of animals. Cattle, in particular, are readily attracted to these " dumps " and consume inordinately large quantities of the earth, or grass growing on it. The result, as some know from experience, is a heavy death-roll.

Prevention of Scab.

The precautions to be taken to prevent the introduction or re-occurrence of sheep scab include the periodic inspection of the sheep, and immediate treatment when the existence of the disease is confirmed. It is advisable always to examine closely all newly-purchased animals, and those returning to the homestead from outside and distant pastures. These sheep should not be permitted to mix with the other flocks until it has been ascertained that no disease exists among them, or until they have been treated thoroughly.

If the sheep are kept in good condition and free from worm infestations, they are less liable to succumb to severe scab infection than sheep in poor condition and diseased. The former can also better withstand immersion.

Many farmers in Kenya, at any rate, keep isolated " hospital " flocks, which comprise sick animals set apart for special treatment and nursing. It is an excellent system contributing to effective control of all diseases and worthy of adoption by all farmers.

Efficient fencing of the farm—and the keeping of fences in good repair—is essential to effective control. In some instances, however, it is a costly undertaking and thus frequently impracticable. Where a number of large, unfenced sheep ranges exist in a district, the alternative to fencing appears to be an agreed policy of simultaneous dipping, supported by a rigid control or prohibition of movement of sheep into that district. There are several practical difficulties in this alternative method, especially where surreptitious movements of native sheep (often moved at night) take place, but determination and zeal might surmount these difficulties.

A scab-eradication campaign cannot be successful without the provision of funds, as it needs an efficient organization to enforce an agreed policy over a protracted period. In most countries the cost of treatment and the responsibility of keeping scab at bay devolve upon the sheep-owners. Expenses incurred in administrative assistance and pressure are borne by the Government concerned. In Basutoland, dipping is free ; but in order to defray the costs, a tax or export duty of one farthing or halfpenny a pound is imposed on all wool exported from the territory.

As the onus of controlling sheep scab falls upon the farmer, he should be thoroughly conversant with every practical aspect of the disease, its treatment and its prevention. The research worker may be able further to enlighten him on several important points which may arise under the particular local conditions. The chemist especially may continue investigations into the question of dips, their preparation and use, their adequacy as a protection against reinfection, and their effect on the wool and the processes in preparing the finished product.

Legal provisions should afford some measure of protection to the zealous farmer from the possible negligence of less progressive neighbours, and, finally, legal safeguards should be provided in as simple a form as possible or made more clear by explanatory leaflets.

I am indebted to Mr. W. A. Pool, Deputy Director of the Imperial Bureau of Animal Health, Weybridge, who has supplied me with notes and literature on sheep scab in different countries ; and who has assisted me with references on the various aspects of the problem.

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EXPLANATION OF PLATE II.

Fig. 1.—Indicating by arrows the lachrymal or infra-orbital pouch and the deeper cavities of the ear. In both sites mites may lurk, and possibly escape the effects of treatment.

Fig. 2.—Showing the " scabs " in the lower part of the ear where many mites were found.

Fig. 3.—Section of a piece of skin and wool, as shown in fig. 4, taken from the back of a sheep which died from a chronic infection of " scab " and emaciation.

Fig. 4.—Section of a piece of skin and wool.

Fig. 5.—Showing a " tag " or " tuft " of wool to which adhere several layers of scabs, and under which were found (at arrow end) a cluster of eggs and live mites.

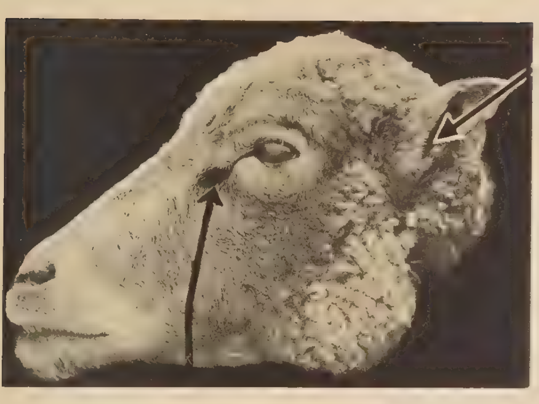

Fig. 1.

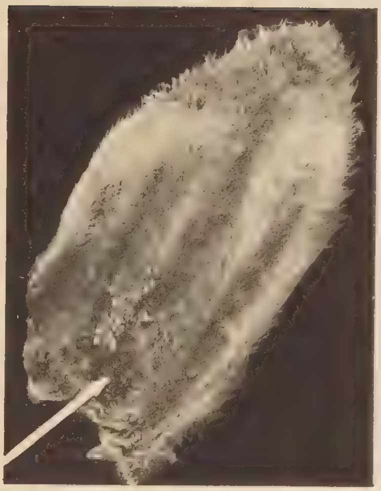

Fig. 2.

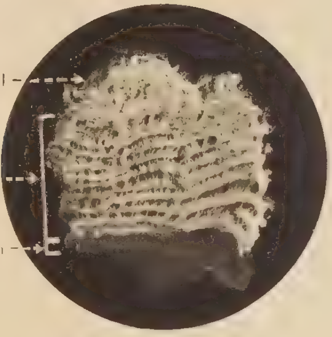
Wool
Layers of scab
Skin

Fig. 3.

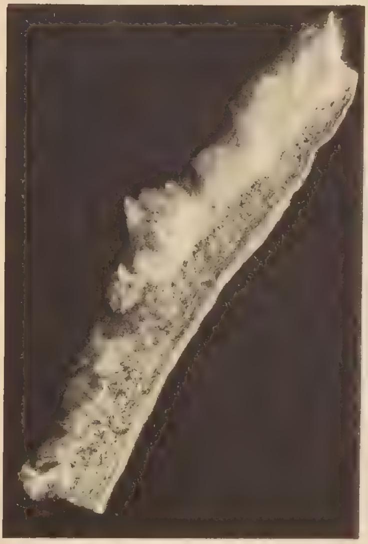

Fig. 4.

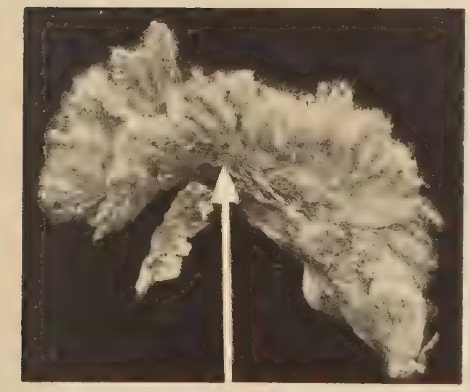

Fig. 5

The [illegible] London.

INCIDENCE OF SHEEP SCAB

THE FOOD OF TSETSE-FLIES (*GLOSSINA SWYNNERTONI* AND *G. PALPALIS*) AS DETERMINED BY THE PRECIPITIN TEST.*

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The data here presented constitute an attempt to subscribe to the intensive study of tsetse-flies now being undertaken in the East African territories. We had originally intended an inquiry into the food of *Glossina palpalis* in various areas of Kenya, but at a general discussion between ourselves and tsetse workers of Uganda and Tanganyika, we gladly agreed with the suggestion of Mr. C. F. M. Swynnerton, Director, Tsetse Research Department, Tanganyika, to extend the inquiry to other species from any part of Eastern Africa.

These first results, though mostly inconclusive, have perhaps narrowed the field of inquiry sufficiently to warrant a continuation of the work along more well-defined lines.

We wish to thank the Director and members of the Tsetse Research Department, Tanganyika, for help in the supply of sera and the collection of *G. swynnertoni*; and the Director, Veterinary Research Laboratory, Nairobi, for buffalo serum. To Mr. W. H. Potts, Senior Entomologist, Tsetse Research, Tanganyika, we are particularly grateful for helpful suggestions in connection with the presentation of results.

Collection of Sera.

Sera were obtained from various sources. The Director and staff, Tsetse Research Department, Tanganyika, provided giraffe, rhino, roan and several others. The Chief Research Officer, Veterinary Research Laboratory, Kabete, provided an excellent supply of buffalo serum from one of his stock animals. All other sera were collected by one or other of our staff.

Animals dealt with by us were shot, and bled into large sterile jars immediately. The jars were allowed to stand overnight to permit the serum to separate. This was then taken off with sterile syringes or pipettes and forced into sterile rubber-capped bottles. We recommended the insertion of a small crystal of thymol to each small bottle of serum that had to travel any considerable distance before arrival at the laboratory in Nairobi.

At the laboratory all sera were filtered (Sietz " E.K."), put into ampoules or sealed tubes and stored in a refrigerator for use.

Preparation of Antisera.

Young, healthy rabbits have been used for the preparation of all antisera. Their treatment consisted of five intravenous injections of 3 cc. normal serum at intervals of 5 or 6 days.

Ten days after the last injection, a small amount of serum was taken off to ascertain its titre. In most cases this was 1 in 1,000 or higher and the rabbit was bled. Occasionally, additional injections have been necessary. Where these have failed to raise the titre, a suspension of sterile powdered tapioca in 3 cc. of the normal serum in use has been injected intraperitoneally. This has usually served to bring the antiserum up to required strength.

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Cross-Reactions.

We carried out cross-reaction tests of all antisera except impala and giraffe, with dilutions of normal sera up to 1 in 1,000 and have shown here only those reactions that are necessary to our attempt at an interpretation of tests on fly stomach contents. Many of these cross-reactions are puzzling. In Table II hartebeeste antiserum reacts to serum of roan but not to its own serum at this dilution. In Table I sheep antiserum does not react with Thomson's gazelle normal serum though Thomson's gazelle antiserum reacts with sheep normal serum. Again buffalo antiserum reacts with normal sera of waterbuck, Thomson's gazelle and hartebeeste, but antisera of these do not react with buffalo normal serum. There are other apparently inexplicable results.

If these results had occurred with the concentrated solutions only, we might have assumed a reason. But they are shown in the reactions of diluted solutions in Table II. Buffalo antiserum reacts with hartebeeste normal serum, but hartebeeste antiserum does not react with buffalo normal serum ; waterbuck antiserum reacts with Thomson's gazelle normal serum, but Thomson's antiserum does not react with waterbuck normal.

Another bewildering result is the reaction of the antisera of some Bovids with the normal sera of others but not with their own. An instance of this is seen in the behaviour of hartebeeste and roan (Table II).

No attempt can be made at present to explain these results.

Preparation of Stomach Contents.

Specimens of *G. palpalis* were obtained by our own staff from Maboko Island in Kavirondo Gulf.

The *G. swynnertoni* were submitted by the Director, Tsetse Research, Tanganyika. All flies were killed by pressure of the thorax and were merely allowed to dry. It is obvious that more exact results would be obtained by dissecting out the stomach from fresh flies.

A certain loss results from the presence in many flies of an excess of fat which renders the "stomach" solution cloudy and therefore unfit for accurate "reading." Further loss probably occurs from continuation of digestive or bacterial action in stomachs after the flies are killed. We hoped to reduce the effect of such losses on results by dealing with a sufficiently large number of specimens.

The abdomen of each fly to be tested is taken off and ground up in the cell of a concave slide with 10 drops of normal saline. This solution is allowed to stand for about an hour at room temperature. It is then taken up in a pipette, transferred to an agglutination tube and centrifuged. In the majority of cases this serves to produce a solution clear enough for testing.

In the first part of this work all fly stomachs were ground up and tested. Later, in order to conserve our antisera, only those stomach solutions showing a " colour " were tested (see page 33). Where an investigation aims at discovering merely the source of blood and not an accurate percentage of a fly population taking such blood, this routine is justified.

Method of Making the Tests.

The tests were carried out in capillary tubes as used for calf lymph. Sufficient of these were taken to provide one for each antiserum in use and one for control. Each antiserum was first drawn into its capillary to about a third of its length. This was followed by about an equal amount of the stomach solution under test. So for each antiserum. Control tubes contained a mixture of stomach contents and normal saline.

All capillary tubes were allowed to stand for one hour at a temperature of 37°C. They were then examined before an obliquely descending light with a black background. Tubes showing definite flocculation or precipitation were recorded as positive. Very weak or doubtful flocculations were recorded as negative for our purposes.

Hosts.

Possible hosts of *G. swynnertoni* are recorded as follows :—Monkey, baboon, rhinoceros, zebra, lion, warthog, leopard, bush-pig, serval, giraffe, cheetah, duiker, civet, oribi, mongoose, steinbuck, hyaena, dikdik, jackal, impala, dog, roan, kudu, eland, antbear and porcupine.

The only possible hosts of *G. palpalis* on Maboko Island appear to be crocodile, hippotamus, Varanus lizards, birds, small rodents and man (the fly boys).

Antisera used.

We have been able to produce antisera of the following :—Ox, buffalo, eland, waterbuck, wildebeeste, Thomson's gazelle, Grant's gazelle, sheep, hartebeeste, roan, impala, pig (domestic), man, zebra, giraffe, horse, hippopotamus, elephant and crocodile. Most of these were used against *G. swynnertoni* ; but only crocodile and hippopotamus against *G. palpalis.*

Limits of this Method.

It is obvious from a comparison of the two preceding paragraphs that except for *G. palpalis* we could not hope to obtain any very considerable number of specific results. It seems probable, in fact, that even by using antisera of all possible hosts an approach to specificity in the Bovids is possible only by a somewhat complicated process of elimination based upon exhaustive cross-reaction tests.

In practical work it was often impossible to clear solutions sufficiently to read weak reactions. That being so, all positive reactions recorded as " traces only " have been ignored. This means a probable loss of considerable numbers of positives, but this can be tolerated if sufficient numbers of flies are being dealt with.

Dilutions of Solutions used.

Our first series of tests against *G. swynnertoni* has been in the main exploratory. They were done with undiluted antisera and " full " strength stomach solutions (*i.e.*, stomach contents macerated in 10 drops of saline). Table I indicates the different bloods to which each antiserum at 1 : 1,000 titre reacts under these conditions.

It is impossible to obtain an accurate measure of the dilution of blood from a tsetse stomach, since the initial amount of blood taken (many flies do not feed to repletion) and the length of time since the last meal are unknown. To some extent this may be overcome, where visible blood occurs, by diluting to a constant light amber or straw colour. This was adopted for the second series of tests.

The presence of colour in a solution of tsetse stomach contents does not invariably indicate the presence of blood. But its absence is so well correlated with the absence of blood (measured by the benzidine test) that we adopted " colour " as a quick and easy indication of " blood " and, as already mentioned, depth of colour as a guide to the dilution of stomach solutions.

It was necessary to decide, however, for an interpretation of Bovid results, to what equivalent stage of dilutions used in the cross-reaction tests these " undiluted "

(1st series) and "amber-diluted" (2nd series) tests corresponded. The first series correspond approximately to cross-reactions carried out with undiluted or 1/10th normal sera and interpretation is based on results of these (Table I). For the second series, however, we compared the reactions, at various dilutions, of artificially fed tsetse stomachs and the appropriate antisera with reactions of homologous normal sera and antisera at similar dilutions.

Tests for *G. palpalis* were carried out with about 1 : 10 stomach solutions against small amounts of normal antisera (of crocodile and hippopotamus).

Interpretation of Results.

We have employed the following process of reasoning for reducing our many combined reactions to reasonable suggestive conclusions.

If the stomach contents of one tsetse-fly reacts to buffalo, Grant's gazelle and giraffe antisera, this indicates that it contains a blood or bloods with some property common to the three bloods of buffalo, Grant's gazelle and giraffe. It may contain blood of all three animals ; but we first assumed the greater probability that it contains the blood of only one animal having a property common to all three.

According to Table I, the common property may be a factor exhibited by either buffalo serum or giraffe serum ; but not by the sera of eland, waterbuck, wildebeeste, ox, Thomson's gazelle, Grant's gazelle, sheep, roan, hartebeeste or impala, since these do not react to all three antisera. Buffalo, however, is not present in the area concerned, though giraffe is.

The stomach of this fly then contained either the blood of a Bovid akin to that of buffalo (but not to the others mentioned above) or the blood of giraffe ; or it may have contained both.

If, however, the stomach contents of one tsetse-fly is tested against the antisera of buffalo, Grant's gazelle and giraffe and reacts only to, say, buffalo, it must contain a property peculiar to buffalo (or the buffalo group) which is not present in Grant's gazelle or giraffe. (If it were present in these two as well, the result would be a combined positive to all three as mentioned above.)

The cross-reactions in Table I indicate that such a property is exhibited in the serum of eland. Since eland is present in the area concerned, we conclude that the fly had definitely fed on eland. In certain cases we have shown the application of this method of elimination.

In the following pages we use the word " group " to indicate a group of animals related by some common precipitating property of their bloods. This relationship may have been previously established, as in the human group, which embraces certain monkeys and baboons, or it may be assumed from the present work. Buffalo, for instance, is one of a very large group of the Bovids related by blood reactions ; eland appears to belong to a very small group, possibly with the ox and kudu ; giraffe seems to be related to a few of the Bovids (*e.g.*, hartebeeste). At the moment we can merely generalise on such groups, perhaps with little justification.

Data on the reactions of roan and impala are particularly scanty. We have ignored them in arriving at possible conclusions.

The results for *G. palpalis* require no such mental strain. Both hippopotamus and crocodile are specific (though the latter may react to monitor lizard and snake blood).

TABLE I.

Indicating the Reactions of certain Antisera to Normal Sera (used at 1 in 10) in the First Series of Tests (compiled from Cross-Reaction Tests).

Antisera	Normal Sera at 1/10 dilution																	
(All brought to 1:1,000 titre)	Eland	Waterbuck	Wildebeeste	Ox	Buffalo	Thomson's Gazelle	Grant's Gazelle	Sheep	Hartebeeste	Roan	Pig	Man	Hippopotamus	Crocodile	Giraffe	Horse	Elephant	Zebra
Eland ...	+	—	—	+	+	—	—	—	—	0	—	—	—	—	0	0	—	—
Waterbuck ...	—	+	—	+	—	+	+	+	—	—	—	—	—	—	—	0	—	—
Wildebeeste ...	—	+	+	+	+	+	+	+	+	—	—	—	—	—	+	0	—	—
Ox	—	—	+	+	+	—	+	+	—	0	—	—	—	—	—	0	—	—
Buffalo ...	+	+	+	+	+	+	+	+	+	—	—	—	—	+	—	0	—	—
Thomson's Gazelle	+	+	+	—	—	+	+	+	—	—	—	—	—	—	—	0	—	—
Grant's Gazelle	—	+	+	+	+	+	+	+	—	+	—	—	—	—	+	0	—	—
Sheep ...	—	+	+	+	+	—	+	+	—	—	—	—	—	—	+	0	—	—
Hartebeeste ...	—	—	+	—	—	—	—	—	+	+	—	—	—	—	+	0	—	—
Roan	0	0	0	0	0	0	0	0	0	+	0	0	0	0	+	0	0	0
Impala ...	0	0	0	0	0	0	0	0	0	+	0	0	0	0	—	0	0	0
Pig	—	—	—	—	—	—	—	—	—	—	+	+	—	—	0	0	—	—
Man	—	—	—	—	—	—	—	—	—	0	—	+	—	—	—	0	—	—
Zebra	—	—	—	—	—	—	—	—	—	0	—	—	—	—	0	0	—	+
Hippopotamus	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	0	—	—
Crocodile ...	—	—	—	—	—	—	—	—	—	0	—	—	—	+	0	0	—	—
Giraffe ...	0	0	0	0	+	0	—	0	+	+	0	0	0	0	+	0	0	0
Horse ...	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	+
Elephant ...	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—

Remarks : 0 indicates that no test was carried out ; — indicates no reaction.

Interpretation of Results with G. swynnertoni (First Series).

Tests were carried out with antisera of various titres and stomach contents equivalent to normal blood at about 1 : 10 dilution.

1. *Eland* (excluding Thomson's gazelle and wildebeeste group).*—Flies tested, 772 ; Number positive, 9=1·2 per cent. (approx.).

Thomson's gazelle antiserum gives positive reactions with its own serum and with eland, waterbuck, wildebeeste, Grant's gazelle and sheep. Wildebeeste antiserum gives positive reactions with its own serum and with waterbuck, ox, buffalo, Thomson's gazelle, Grant's gazelle, sheep, hartebeeste and giraffe.

These single positives to eland, therefore, cannot indicate the presence of eland blood, for, if this had been present, positives would have been obtained with Thomson's gazelle which also reacts to eland. That is, the result would have been *double* positives. For the same reason they cannot indicate the presence of any of the other bloods to which antisera of Thomson's and wildebeeste react. They therefore indicate some Bovid not in our range.

2. *Thomson's gazelle* (excluding wildebeeste group).—Flies tested, 1,733 ; No. positive, 1=0·06 per cent.

The property present in Thomson's gazelle, which is not present in wildebeeste, is one exhibited by the eland group (possibly kudu).

3. *Wildbeeste* (excluding Thomson's gazelle group).—Flies tested, 1,733 ; No. positive, 153=9 per cent. (approx.).

Wildebeeste antiserum reacts to its own serum and to waterbuck, ox, buffalo, Thomson's gazelle, Grant's gazelle, sheep, hartebeeste and giraffe. Thomson's gazelle reacts to its own serum and to waterbuck, wildebeeste, Grant's gazelle and sheep. If any of these last bloods had been present the results would have been *double* positives (*i.e.*, to wildebeeste and Thomson's). They are, therefore, eliminated. This leaves ox, buffalo, hartebeeste and giraffe as the possible bloods, these being represented by wildebeeste but not by Thomson's gazelle.

Positives to ox and buffalo, which are absent from the area concerned, may indicate some Bovid, such as the kudu, which is present. The hartebeeste factor, if it is significant, may be associated with such a Bovid or with giraffe, whilst giraffe may indicate actual giraffe or a related Bovid such as hartebeeste. Hence we conclude that these positives may be a Bovid of the ox-buffalo group (? kudu) or of the hartebeeste group or giraffe, or of more than one of these.

4. *Wildebeeste* (including Thomson's gazelle group).—Flies tested, 782 ; No. positive, 286=36 per cent.

These may indicate one or more of a group which includes waterbuck, wildebeeste, ox, buffalo, Thomson's gazelle, Grant's gazelle, sheep, hartebeeste or giraffe. But since in (2) there is only one positive to the Thomson's gazelle group containing all these except ox, hartebeeste and giraffe groups, it seems probable that the majority of these 286 positives are one or more Bovids, not in our range, of the ox or hartebeeste group, or giraffe.

5. *Grant's gazelle* (excluding giraffe and buffalo groups).—Flies tested, 26 ; No. positive, nil.

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* Throughout these notes :—Excluding = tested in the presence of Thomson's gazelle antiserum and reacting only to wildebeeste.
Including = not tested in the presence of Thomson's gazelle antisera and therefore may include any or all of the group reacting to Thomson's gazelle, except eland.

6. *Giraffe* (excluding Grant's gazelle and buffalo groups).—Flies tested, 26 ; No. positive, 1.

Since Grant's and buffalo gave no positives, this one positive indicates a host outside the range of our cross-reactions.

7. *Buffalo* (excluding giraffe and Grant's groups).—Flies tested, 26 ; No. positive, nil.

8. *Buffalo and Grant's gazelle* (excluding giraffe group).—Flies tested, 26 ; No. positive, 4.

Here the factors producing the positive results must be present in both buffalo and Grant's gazelle blood groups, but not in the giraffe group. They may be some property of the bloods of waterbuck, wildebeeste, ox, buffalo, Thomson's gazelle, Grant's gazelle or sheep, since these react to both antisera, but not of eland or hartebeeste since these do not react to both antisera. None of the animals possessing this property exists in the area concerned. The positives, therefore, indicate some Bovid not in our range.

9. *Buffalo, giraffe and Grant's gazelle.*—Flies tested, 26 ; No. positive, 2.

The factor common to these three occurs in buffalo and giraffe sera. Positives, therefore, indicate the giraffe group or a Bovid not in our range (since buffalo itself is not present in the area) or both.

10. *Buffalo and pig* (excluding Grant's gazelle and giraffe groups).—Flies tested, 26 ; No. positive, 1.

Pig and a Bovid of the eland or hartebeeste groups.

11. *Buffalo, Grant's gazelle and pig* (excluding giraffe).—Flies tested, 26 ; No. positive, 1.

A Bovid (not eland or hartebeeste groups) and pig.

12. *Human group* (excluding pig).—Flies tested, 2,412 ; No. positive, 85.

These are monkey or baboon (or human) or both.

13. *Pig* (excluding human group).—Flies tested, 2,250 ; No. positive, 168.

These are pig.

14. *Pig* (including human group).—Flies tested, 172 ; No. positive, 5.

These may be pig or human group (*i.e.*, monkey or baboon) or both.

15. *Zebra.*—Flies tested, 1,065 ; No. positive, nil.

16. *Waterbuck.*—Flies tested, 172 ; No. positive, 11.

These are one or more of many Bovids.

17. *Eland and wildebeeste* (excluding Thomson's gazelle group).—Flies tested, 656 ; No. positive, 9.

These are a Bovid of the ox-buffalo group.

18. *Eland, wildbeeste and Thomson's gazelle.*—Flies tested, 656 ; No. positive, 6.

Since there appears to be no property within our range common to all three, these positives suggest a Bovid (not eland) group beyond our range.

19. *Thomson's gazelle and wildebeeste* (excluding eland group).—Flies tested, 497 ; No. positive, 4.

Bovid ; not eland or buffalo group, nor hartebeeste, nor giraffe.

20. *Thomson's and wildebeeste* (including eland group).—Flies tested, 783; No. positive, 39.

Bovid, but not eland, buffalo, hartebeeste or giraffe groups.

21. *Eland, human, Thomson's gazelle and wildebeeste.*—Flies tested, 484; No. positive, 4.

Anti-human sera do not react to Bovid sera. Positives to this as well as to Bovid indicates the presence of blood of both the human, monkey, baboon and Bovid groups. Regarding the latter, there is no factor in our cross-reactions common to the three bloods of eland, Thomson's gazelle and wildebeeste. The Bovid blood is therefore of some animal beyond our range.

22. *Wildebeeste and pig* (excluding human group).—Flies tested, 667; No. positive, 68.

Bovid or giraffe with pig.

23. *Wildebeeste and pig* (excluding Thomson's gazelle group and human group).—Flies tested, 243; No. positive, 9.

Bovid in the buffalo or hartebeeste groups, or giraffe, with pig.

24. *Eland, human and wildebeeste.*—Flies tested, 159; No. positive, 1.

Human group (monkey or baboon) and a Bovid of the buffalo group (not eland or giraffe).

25. *Pig, Thomson's gazelle and wildebeeste* (excluding human group).—Flies tested, 238; No. positive, 3.

Pig with a bovid (not eland or buffalo groups, nor giraffe or hartebeeste).

26. *Human, pig, Thomson's gazelle and wildebeeste.*—Flies tested, 240; No. positive, 2.

Probably pig (or human group with pig) and a Bovid not in our range (since Thomson's gazelle alone has given only one positive in 1,750).

27. *Human, pig and wildebeeste* (excluding Thomson's gazelle).—Flies tested, 241; No. positive, 8.

Pig (or human group with pig) and a Bovid, not in our range, of the buffalo-ox group or hartebeeste or giraffe groups.

Summary of Tests with G. swynnertoni (First Series).

1.	Total of flies tested, 2,703.		
	,, ,, ,,	discarded (with no obvious blood), 2,269	
2.	,, ,, ,,	with blood of *human group* (man, monkey, baboon),	
		Single positives	85
		Combined with other bloods	5
		Doubtful	18
3.	,, ,, ,,	with blood of *pig*,	
		Single positives	168
		Combined with other bloods	79
		,, and doubtful	18
4.	,, ,, ,,	with blood of *eland* or related Bovid,	
		Single positives	9
5.	,, ,, ,,	with blood of *giraffe* or relation,	
		Combined and doubtful	517
6.	,, ,, ,,	with blood of a Bovid not in our range,	
		Combined	635
7.	,, ,, ,,	with blood of *zebra*	nil.

Conclusion.—The most important food hosts appear to be a big Bovid, not closely related to eland or to smaller ovines, and giraffe or a close relation. Pig and monkeys and/or baboons are not unimportant; but zebra are apparently not even slightly concerned.

Indicating the Reactions of certain Antisera to Normal Sera (used at 1/400) in the Second Series of Tests (compiled from Cross-Reaction Tests).

Antisera at 1 in 1,000 titre	Normal Sera at 1 in 400																	
	Eland	Waterbuck	Wildebeeste	Ox	Buffalo	Thomson's Gazelle	Grant's Gazelle	Sheep	Hartebeeste	Roan	Pig.	Man	Zebra	Hippopotamus	Crocodile	Giraffe	Horse	Elephant
Eland ...	+	–	–	+	–	–	–	–	–	0	–	–	–	–	–	0	0	–
Waterbuck ...	–	+	–	–	–	+	–	+	–	–	–	–	–	–	–	–	0	–
Wildebeeste ...	–	–	–	+	+	–	–	+	–	–	–	–	–	–	–	–	0	–
Ox	–	–	–	+	+	–	–	–	–	0	–	–	–	–	–	–	0	–
Buffalo ...	+	+	+	+	+	+	+	+	+	–	–	–	–	–	–	–	0	–
Thomson's Gazelle	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	0	–
Grant's Gazelle	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	0	–
Sheep	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	0	–
Hartebeeste ...	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	+	0	–
Roan	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	+	0	0
Impala ...	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	–	0	0
Pig	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	0	0	–
Man	–	–	–	–	–	–	–	–	–	0	–	+	–	–	–	–	0	–
Zebra	–	–	–	–	–	–	–	–	–	0	–	–	+	–	–	0	0	–
Hippopotamus	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	0	–
Crocodile ...	–	–	–	–	–	–	–	–	–	0	–	–	–	–	+	0	0	–
Giraffe ...	0	0	0	0	–	0	–	0	–	–	0	0	0	0	0	+	0	0
Horse ...	–	–	–	–	–	–	–	–	–	0	–	–	+	–	–	0	0	–
Elephant ...	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–	0	0	+

Remarks : 0 indicates that no test was carried out; – indicates no reaction.

Interpretation of Results with G. swynnertoni (Second Series).

Tests were carried out with stomach contents diluted to amber or straw colour (equivalent to 1/400 blood) and antisera at 1 in 1,000 titre (Table II).

1. *Buffalo* (excluding giraffe, Grant's, human, pig, zebra).—Flies tested, 303 ; No. positive, 3.

   These may be eland or something akin.

2. *Giraffe* (excluding buffalo and Grant's gazelle).—Flies tested, 303 ; No. positive, 39.

   These can be only giraffe (or something closely related, other than hartebeeste).

3. *Human.*—Flies tested, 303 ; No. positive, 6.

   These are human group (baboon or monkey).

4. *Pig.*—Flies tested, 303 ; No. positive, 48.

5. *Zebra.*—Flies tested, 303 ; No. positive, nil.

6. *Buffalo and Grant's gazelle* (excluding giraffe).—Flies tested, 303 ; No. positive, 14.

   These are a Bovid (not eland or ox) reacting to buffalo, not in our range.

7. *Human and pig.*—Flies tested, 303 ; No. positive, 1.

   This is human group and pig.

8. *Buffalo, giraffe and Grant's gazelle.*—Flies tested, 303 ; No. positive, 58.

   These indicate a Bovid not in our range, with or without giraffe.

9. *Buffalo and giraffe.*—Flies tested, 303 ; No. positive, 1.

   This is probably a Bovid with or without giraffe.

10. *Giraffe and Grant's gazelle.*—Flies tested, 303 ; No. positive, 20.

    Probably a Bovid outside our range, with or without giraffe.

11. *Buffalo, giraffe, Grant's gazelle and pig.*—Flies tested, 303 ; No. positive, 1.

    This indicates pig with a Bovid not in our range, or with giraffe, or with both.

Summary of Second Series.

1. Total of flies tested, 303.
   ,, ,, ,, discarded, no obvious blood, 702.
2. ,, ,, ,, with blood of a Bovid of the ox-buffalo or hartebeeste group,
   Single positives ... ... 3 (1 per cent.)
   Combined ... ... 74 (24 per cent.)
3. ,, ,, ,, with blood of giraffe or something closely related,
   Single positives ... ... 39 (12 per cent.)
   Combined and doubtful ... 80
4. ,, ,, ,, with blood of human group (monkey, baboon),
   Single positives ... ... 6 } 2 per cent.
   Combined ... ... 1 }
5. ,, ,, ,, with blood of pig,
   Single positives ... ... 48 } 17 per cent. (approx.
   Combined ... ... 2 }
6. ,, ,, ,, with blood of zebra ... ... Nil.

Conclusion.—Hosts in order of importance appear to be (*a*) one or more Bovids outside our range, related to buffalo or hartebeeste (and possibly to giraffe) ; (*b*) giraffe ; (*c*) pig ; (*d*) monkey and/or baboon. Zebra is again not implicated.

General Summary of Tests with G. swynnertoni.

Total flies examined,	6,017
,, ,, discarded,	3,011
,, ,, tested,	3,006

Percentage of flies examined positive to
(*a*) Human group (monkey, baboon) (not including doubtfuls) = 3
(*b*) Pig (not including doubtfuls) = 9
(*c*) Giraffe or near relative = 0·6
combined or doubtful = 19
(*d*) Bovid (not in our range), combined and doubtful = 23
(*e*) Zebra = nil.

Tests with G. palpalis on Maboko Island.

We have used only two antisera (crocodile and hippopotamus) with a very occasional third (human) in tests of the stomach contents of this species. Results, therefore, are fairly definite and we have considered it necessary to show only a summary of our findings (see Table III).

TABLE III.

Showing Results of Precipitin Tests on Stomach Contents of G. palpalis *on Maboko Island.*

Month and year caught	Species	Total number examined	Positive to crocodile antiserum		Positive to hippopotamus antiserum	
			No.	Percentage	No.	Percentage
October 1932	*G. palpalis*	627	46	7·3	24	3·8
November 1932 ...	do.	130	16	12·3	2	1·5
December 1932 ...	do.	76	7	9·2	1	1·3
January 1933 ...	do. do. (Headland, Maboko)	547 507	39 8	7·1 1·57	15 2	2·7 0·4
February 1933 ...	*G. palpalis*	500	28	5·6	20	4·0
April 1933	do.	925	38	4·1	22	2·4
May 1933	do.	396	21	5·3	24	6·06
January 1934 ...	do.	188	nil	nil	2	1·06
April 1934	do.	376	11	2·9	4	1·06
May 1934	do.	275	3	1·09	nil	nil
July 1934	do.	596	18	3·02	6	1·01
August 1934	do.	676	2	0·29	9	1·33
Total		5,819	237	4·07	131	2·25
Total Minus Headland Catches ...		5,312	229	4·31	129	2·43

It should be kept in mind that positive reactions to crocodile antiserum, however, may indicate the presence of snake or lizard blood as well as crocodile ; but it fails to react to the blood of the hen—our only representative of birds. Hippopotamus antiserum, so far as we have ascertained, is specific.

It is perhaps remarkable that the percentage of positives to these two very large and accessible animals is so low. Undoubtedly our figures are lower than they might be because we have ignored " traces." Moreover, the precipitin method fails to determine a blood meal that is more than 3 days old. Allowing for these points, however, there appear to be large numbers of flies that have not fed on the two most obvious hosts.

On what have they fed ? There are indications that birds, or some factor associated with birds, are an attraction. On Maboko there is a large colony of cormorants and several smaller groups of egrets. Pythons were frequently seen below the cormorant colony ; small lizards have been seen apparently robbing the nests ; and crocodiles possibly lie up waiting for unwary fledglings. Before flies had been reduced in numbers by trapping, fly density was much greater in the vicinity of the bird colonies than in other portions of the infested shore belt.

We had hoped to be able to produce a cormorant antiserum to decide this question ; but we have failed to obtain sufficient blood for the purpose—these birds are particularly bloodless. We have attempted to produce an antiserum from extracts of various organs. This has also not been successful.

Summary.

1. The main food hosts of *Glossina swynnertoni* in a district of Tanganyika appear to be (*a*) one or more Bovids, perhaps kudu or roan, exhibiting a close blood relationship to ox or buffalo ; (*b*) giraffe ; (*c*) pig. There is evidence that monkey or baboon is also made use of and that zebra definitely is not.

2. With regard to *G. palpalis* on Maboko Island, crocodile and hippopotamus are important hosts. But they are far less important than we had supposed. The majority of flies appear to have fed on some animal not yet determined.

COCCID-INHABITING PARASITES FROM AFRICA WITH DESCRIPTIONS OF NEW ENCYRTIDAE AND APHELINIDAE.*

By Harold Compere,

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The species of Encyrtidae and Aphelinidae described as new or listed in this paper were among a lot of Coccid-inhabiting parasites received from the Entomological Branch, Department of Agriculture, New South Wales. This material was obtained in Kenya and Uganda during August to October 1935 by William B. Gurney, Entomologist, Department of Agriculture, N.S.W., mostly from *Ceroplastes* spp. Except for *Scutellista* sp., only species of Encyrtidae and Aphelinidae are reported upon in this paper. Mr. Gurney visited Kenya and Uganda for the purpose of finding and despatching living parasites of White Wax Scale (*Ceroplastes* spp.) in East Africa to establish in New South Wales for control of White Wax Scale of citrus trees and shrubs. While in Africa he arranged for Mr. H. Wilkinson, Entomologist, Kenya, and Messrs. H. Hargreaves and T. H. C. Taylor, Entomologists in Uganda, to continue to despatch further consignments of parasitised White Wax Scale after he had left.

In the letter from N. S. Noble, Assistant Entomologist, accompanying the specimens, he stated that in New South Wales *Scutellista cyanea*, Motsch., had never been known to attack wax scales, although it is common there as a parasite of *Saissetia oleae* (Bern.), but that the form of *Scutellista* introduced from Kenya, where it was obtained from *Ceroplastes*, has freely reproduced in wax scales in New South Wales. Because of the possible economic importance of the *Ceroplastes*-inhabiting *Scutellista*, an effort was made to distinguish between it and the *Saissetia*-inhabiting form.

The holotypes and allotypes of the new species are to be deposited in the British Museum and paratypes in the United States National Museum.

Family Encyrtidae.

Diversinervus elegans, Silvestri.

Diversinervus elegans, Silvestri, Boll. Lab. Zoöl., Portici, **9**, 303–305, 1915; Compere, H., Univ. Calif. Publ. Entom., **5** (11), 241–245, 1931.

Cheiloneuroides bicristatus, Girault, Mem. Queensland Mus., **4**, 96–97, 1915.

Diversinervus meridionalis, Compere, H., Univ. Calif. Publ. Entom., **5** (11), 237–239, 1931.

Fourteen ♀♀ from *Ceroplastes* sp., from Kenya Colony, October and December 1935.

Diversinervus elegans is a primary parasite. The samples obtained from *Ceroplastes* in Kenya and those collected by S. E. Flanders in Australia appear morphologically indistinguishable from samples of *D. elegans* reared from *Saissetia oleae* collected at Nefasit, Eritrea, the type locality. In the collection of the Citrus Experiment Station are specimens from Australia as follows: a single specimen, determined by Girault as *D. bicristatus*, bearing the label " on black scale, Brisbane,

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* Paper No. 357, University of California Citrus Experiment Station and Graduate School of Tropical Agriculture, Riverside, California.

Queensland, August 27, 1900, George Compere." One female from *Saissetia* collected by Flanders at Sydney, 15th June 1931; two females and one male ex *Saissetia* sp. on orange, Goodu Station, Queensland. Flanders states that *D. elegans* was abundant at Coff's Harbour, New South Wales, where he noticed it working on *Saissetia nigra* (Nietn.) infesting guavas. *Diversinervus meridionalis*, Compere, appears to be a synonym of *D. elegans*, Silvestri.

Genus **Coccidoxenus,** Crawford.

Coccidoxenus, Crawford, Proc. U.S. Nat. Mus., **45,** 248, 1913.

The species *ugandensis*, described in this paper under *Coccidoxenus*, is congeneric with three African species, *coelops*, *obscuratus*, and *distinguendus*, described by James Waterston. It is debatable whether these species should be classified under *Coccidoxenus*. The Neotropical species of *Coccidoxenus*, as represented by *portoricensis*, Crawford, the genotype, and several other closely related, undescribed species from Brazil, differ rather fundamentally from the African species. In the Neotropical species the head is not coarsely punctate, and the frontovertex is provided with fine setigerous punctations arranged in four more or less regular rows; the scrobes are not deep and angularly convergent above but shallow, rounded above, and usually with a faint fossa on either side of the median line; the marginal vein is not punctiform but twice as long as wide. With one exception the Neotropical species lack a cross band of refractive cilia on the forewings.

Since the erection of the genus *Coccidoxenus* by Crawford in 1913, twenty-five species have been described under this name. Girault has described eighteen species from Australia, few if any of which are correctly placed, since he considered *Coccidoxenus* as intergrading with *Anagyrus* and described *Anagyrus*-like species under *Coccidoxenus*. Two species from Europe have been described by Mercet under *Coccidoxenus*. From Mercet's description and figure of *cupratus*, it appears as though it is more closely related to the African species than to the Neotropical species. The other species described by Mercet is known in the male sex only.

Coccidoxenus was incorrectly classified by Crawford. It is not an Ectromine genus, nor is it comparable with or closely related to *Anagyrus*, *Taftia*, and *Anusia*, as stated. The undescribed South American species, which are closely related to the genotype *portoricensis*, suggest the relationship of these species to *Microterys*, as represented by some of the large, partly metallic species.

Key to the African Species of Coccidoxenus, *Females.*

1. Cheeks without coarse punctations posterior to the genal sulci 2
   Cheeks with coarse punctations posterior to the genal sulci; wings not infuscated ... ... *coelops*, Waterston
2. Integument of head with punctations in the area between the anterior ocellus, orbits, and scrobes 3
   Integument of head without punctations in the area between the anterior ocellus, orbits, and scrobes ... ... *distinguendus*, Waterston
3. Frontovertex at narrowest part one-sixth as wide as the head. Forewings faintly tinted beyond the clear cross band ... *obscuratus*, Waterston
   Frontovertex at narrowest part one-fourth as wide as the head. Forewings hyaline beyond the clear cross band ... ... *ugandensis*, sp. n.

Coccidoxenus ugandensis, sp. nov.

♀. Dominantly black metallic; cheeks posterior to the sulci, scutellum, propodeum laterad of the spiracles and basal tergite refringent greenish blue; head somewhat variable, frontovertex and face more or less bluish green blended with violaceous, the scrobes cupreous ; mesoscutum less brilliant than the scutellum and with blended bluish green and violaceous reflections ; antennae brown diluted with fuscous ; first four tarsal joints of middle and hind legs sordid whitish, those of forelegs pale brown ; knees brownish ; shortly exserted ovipositor-sheaths brown ; otherwise black or nearly so.

Head, dorsal view, a trifle more than twice as wide as long (15 : 7) ; frontovertex relatively wide, slightly more than one-fourth the width of head (4 : 15) ; ocelli in an equilateral triangle, the anterior ocellus about three times its own diameter from the orbits, the posterior pair about once their diameter from the occipital margin and almost contiguous with the orbits ; the coarse punctations are smaller than the diameter of an ocellus. In the species illustrated by Waterston, the punctations are shown close together, while in this species, except for the orbital rows, the punctations on the frontovertex, face, and cheeks are spaced almost their own diameters apart. Scrobes deep, narrow, with a small median fossa within the angle formed at their convergence above.

Antennal scape slender, six times as long as wide, widest near the middle ; pedicel twice as long as wide and a trifle longer than the first funicle joint ; funicle joints almost subequal in length and gradually increasing in width, the first twice as long as wide, the sixth a trifle wider than long ; club elongate oval, rounded at the apex, almost twice as long as wide and a trifle shorter than the three preceding funicle joints combined.

Forewings closely resemble those of *coelops*, as figured by Waterston, except that in this species the wings are slightly broader, being approximately two and one-half times as long as wide instead of almost three times as long as wide ; a distinct fuscous cloud occurs beneath the stigma, and the cross band of refractive cilia is separated from the anterior wing margin.

Length, 1·8 mm.

Described from four ♀♀, holotype and paratypes, ex *Ceroplastes destructor*, Newst., Uganda, 20.x. and 29.xii.1935 (*T. H. C. Taylor*).

Genus **Bothriophryne**, nov. (fig. 1).

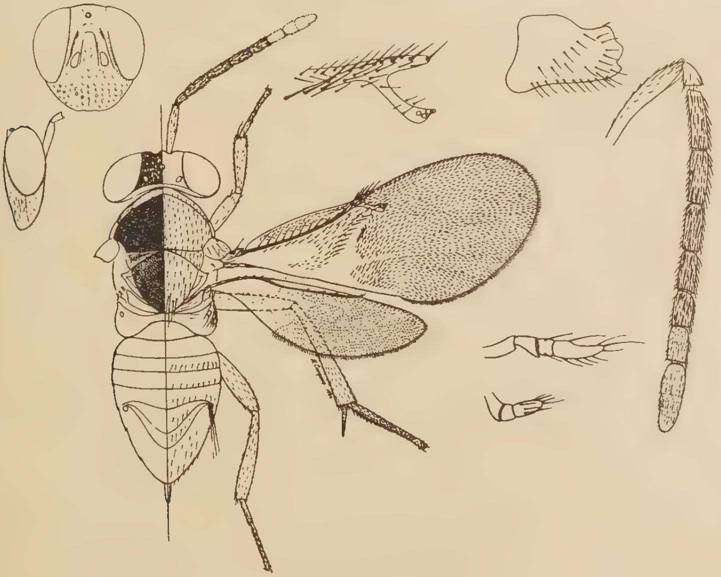

Fig. 1. *Bothriophryne ceroplastae*, sp. n. ♀.

The genus *Bothriophryne* is erected for a group of African Coccid-inhabiting species, one of which is described in this paper, and four of which remain undescribed. The undescribed species were reared from *Ceroplastes* spp. and *Pulvinaria* sp., by E. W. Rust, in Natal during 1925 and 1926.

The species of *Bothriophryne* can be distinguished most readily by the following characters : antennae inserted near the middle of the face well above the basal ocular line ; funicle joints long ; club short ; scape when in repose extending upward beyond the horizontal plane of the head ; scrobes deeply grooved with steep sides ; head in dorsal aspect presenting a view of the median prominence between the scrobes. In wing and body characters, the species of *Bothriophryne* do not appear unlike the African species classified under *Coccidoxenus*, nor unlike those classified under *Baeoanusia*, Girault.

Genotype : *Bothriophryne ceroplastae*, sp. nov. (fig. 1).

Bothriophryne belongs to a group of genera, the species of which are Coccid-inhabiting and possess the following diagnostic characters :

Moderately large-sized species, ranging near 2·0 mm. in length ; dominantly dark metallic with variable reflections ; scutellum often bright bluish green or violaceous ; base of the abdomen in the dorsum highly refringent bluish green to violaceous ; sides of propodeum with tufts of sparse, soft, white setae which become transparent in balsam ; face and cheeks with small, flattened, whitish setae that arise from the centre of shallow, refringent punctations. Eyes large, mostly vertical, glabrous. Thorax strongly convex ; scutellum large, rounded at apex, the apex with sparse semi-erect setae. Mesoscutum finely reticulated without punctations comparable to those on the head ; scutellum more coarsely reticulated than the mesoscutum. Mandibles with a well-defined ventral tooth and a broad truncation which may or may not give a tridentate effect. Labial palpi three-jointed ; maxillary palpi four-jointed. Antennae variable, eleven-jointed, self-coloured or parti-coloured. Abdomen often elongate and semi-triangular, in tag mounts after shrinkage definitely triangular ; ovipositor usually more or less exserted, enclosed by the ventrites to the apex of the abdomen.

The genera known to me, which fall within this diagnosis, can be separated by the following key.

Key to some Genera of Metallic Encyrtids, with Punctations on the Head, that Inhabit Soft Coccids.

1. Scrobes narrow, deeply grooved, with steep sides 3
   Scrobes wider, shallow, with gently sloping sides 2
2. Antennae strongly clavate, the club about as long as the funicle ; funicle joints short, transverse ; pedicel much larger than the first funicle joint ; scutellum convex but not raised above the horizontal plane of the mesoscutum. African species ... ... *Baeoanusia*, Girault
   Antennal club small, slightly wider than the funicle and about as long as the two preceding joints ; funicle joints longer than wide ; subequal to the first funicle joint ; scutellum strongly convex, elevated above the horizontal plane of the mesoscutum. Neotropical species ... *Coccidoxenus*, Crawford
3. Antennae inserted below the middle of the face, about half-way between the orbits and the oral margin. Funicle joints not especially long, the club plainly wider than the funicle and longer than the first funicle joint. Forewings often with a cross band of refractive cilia. African species *Coccidoxenus*, Crawford
4. Antennae inserted near the middle of the face, the sockets above the basal ocular line. Funicle joints long ; the club small, not much wider than the funicle nor longer than the first funicle joint ... *Bothriophryne*, gen. nov.

Bothriophryne ceroplastae, sp. nov. (fig. 1).

♀. Face below the antennal sockets dark violaceous, the frontovertex with mostly dark bluish green reflections. Scape brown; flagellum fuscous, except slightly towards the apex of pedicel; apex of fifth funicle joint, the entire sixth funicle joint and club which are yellowish white. Scutellum bluish green; mesoscutum black with faint bluish green and violaceous reflections; pronotum and axillae black without bright reflections; first tergite partly smooth, highly refringent bluish green; propodeum laterad of the spiracles slightly refringent bluish green with white, soft setae. Middle and hind legs with the tibiae and tarsi and distal ends of femora white to pale yellowish; front legs with the tibiae and tarsi and distal ends of the femora pale brown. Distal ends of the ovipositor-sheaths pale brown.

Head, dorsal view, slightly more than twice as wide as long (21 : 9), frontovertex slightly more than one-third the head width (8 : 21), ocelli in a slightly obtuse triangle; in frontal view the head is slightly wider than high (21 : 19), the eyes reach downward about three-fourths the depth (14 : 19). Antennae inserted well above the basal ocular line, about a socket's length apart. When in repose the scape projects one-half its own length beyond the scrobes.

Other parts as shown in fig. 1.

♂. Coloured similarly to the ♀, except that the sixth funicle joint is fuscous, concolorous with those preceding and the club is brown, suffused with fuscous.

Head, dorsal view, three times as wide as long, the frontovertex occupying one-half the width, coriaceous, with faint setigerous punctations; ocelli in a strongly obtuse triangle, the posterior pair almost touching the occipital margin and separated from the orbits by less than one-half their own diameter. Head (frontal view) as wide as high; antennae inserted near the middle, the base of the sockets above the basal ocular line.

Scape somewhat shorter than in the female, widest towards the apex, pedicel small, about as long as wide; funicle joints slender, all longer than wide, decreasing in length distally, the first about four times as long as wide and as long as the club, the sixth less than twice as long as wide; club small, three-jointed. Flagellum with moderately long, curved, fuscous setae.

Described from 2 ♀♀ and 4 ♂♂, holotype, allotype, and paratypes. The holotype reared from a large *Ceroplastes* sp. on *Clerodendron* sp., Kampala, Uganda, 10.x.1935. The other ♀ was obtained from *Ceroplastes destructor*, Newst., questionably on citrus, Uganda, 1.x.1935.

Anicetus parvus, sp. nov. (fig. 2).

This species can be distinguished from six previously described species and four undescribed species by the following diagnostic characters: Ovipositor exserted less than one-third the length of the abdomen; dorsal face of pedicel convex and setose; frontovertex smooth and polished anterior to the median ocellus; pedicel greatly enlarged, almost as wide as the sixth funicle joint; dorsal and ventral margins of flagellum with coarse, lamellated black setae; posterior tibiae with two fuscous spots or bands.

What appears to be a fifth undescribed species of *Anicetus* agrees with *parvus* in all the diagnostic characters mentioned above. Apparently these two closely related forms can be separated by the comparative lengths of the ovipositors as seen in semi-transparent slide-mounted specimens. In *parvus* the over-all length of the ovipositor is fully equal to the length of the abdomen and is nearly as long as the tibiae and tarsal joints of the hind legs combined. In the undescribed South African species the over-all length of the ovipositor is plainly less than the length of the abdomen and only slightly longer than the hind tibiae.

♀. General colour pale brownish to orange-yellow; mesoscutum with faint purplish reflections; sides of metanotum, concealed part of pronotum, and base of abdomen, partly brown or blackish; basal corners of abdomen slightly metallic; face and cheeks with a narrow, transverse band at the level of the antennal sockets; face and cheeks lemon-yellow above the cross band and sordid white below; antennae mostly orange-yellow, the club fuscous except towards the base, the radical joint completely and the ventral margin of the scape narrowly bordered with blackish; posterior tibiae with two blackish or brownish bands or partly encircling spots; basitarsus of posterior legs partly fuscous, the apical tarsal joint entirely so; middle tibiae with a small brown or fuscous blotch beneath near the apex.

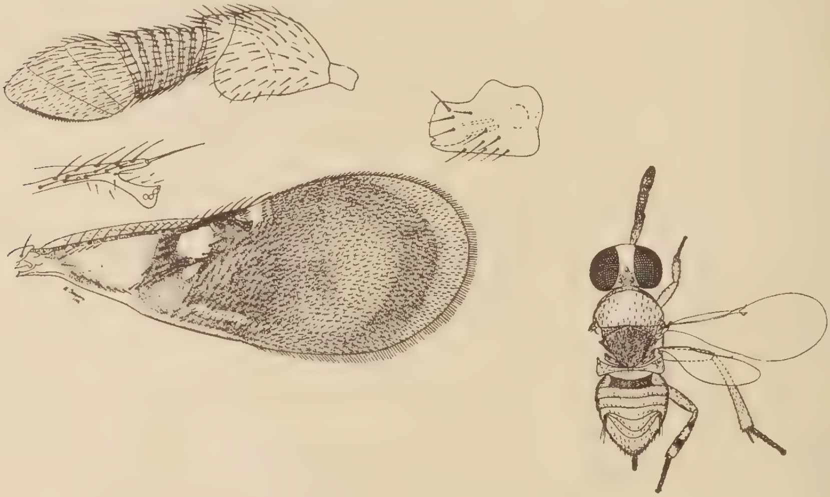

Fig. 2. *Anicetus parvus*, sp. n. ♀.

Frontovertex three times as long as wide, at the narrowest part one-fifth of the head width; ocelli in an equilateral triangle or nearly so, the anterior ocellus about its own diameter from the orbits; ocellar space subopaque, finely reticulate punctate; anteriorly the frontovertex is polished with faint purplish reflections.

Scape large, the ventral margin with a slight inflexion near the middle.

Antennae, forewings, stigmal, marginal and postmarginal veins, mandibles, and general shape and proportions of head and body as shown in figure 2.

Described from 2 ♀♀, holotype and paratype, from small *Ceroplastes destructor*, Newst., on coffee, Kampala, Uganda, 1, 4.x.1935.

The life-history of one species of *Anicetus* is known. *A. annulatus*, Timb., is a primary parasite of certain Lecaniine Coccids. Presumably the other species will prove to have similar host relations.

Cerapterocerus inutilis, sp. nov. (fig. 3).

This species differs from typical *Cerapterocerus* by the same combination of characters which Tei Ishii used to define his genus *Metacerapterocerus*, namely, . . . " forewings not so elongate; marginal vein short; postmarginal vein present, almost as long as the stigmal vein; submarginal vein without a triangular expansion at the apical third." The antennae of the species described here are comparable with those of *Cerapterocerus mirabilis*, Westwood, the genotype, and are unlike the antennae of *Metacerapterocerus*. According to Ishii's description, in *Metacerapterocerus* the pedicel is large, one-half as long as the scape, and only slightly shorter than the funicle. In this species, as in typical *Cerapterocerus*, the pedicel is relatively small. Possibly *C. inutilis* is intermediate between typical *Cerapterocerus* and *Metacerapterocerus*.

♀. General colour black with reflections and admixtures of bluish, greenish, and violaceous. The frontal aspect of the head is almost entirely bright bluish with admixtures of green and violaceous. Mesoscutum and disk of scutellum with greenish reflections dominant, the sides of the latter with dominantly bluish reflections. Tegulae dark brown to blackish. Exserted ovipositor-sheaths tipped at ends with pale brown. First and fifth tarsal joints of all legs blackish, the intermediate joints light brown ; distal ends of front and middle tibiae light brown ; remainder of the legs black. Antennae black. Forewings with an infuscated pattern as shown in figure 3.

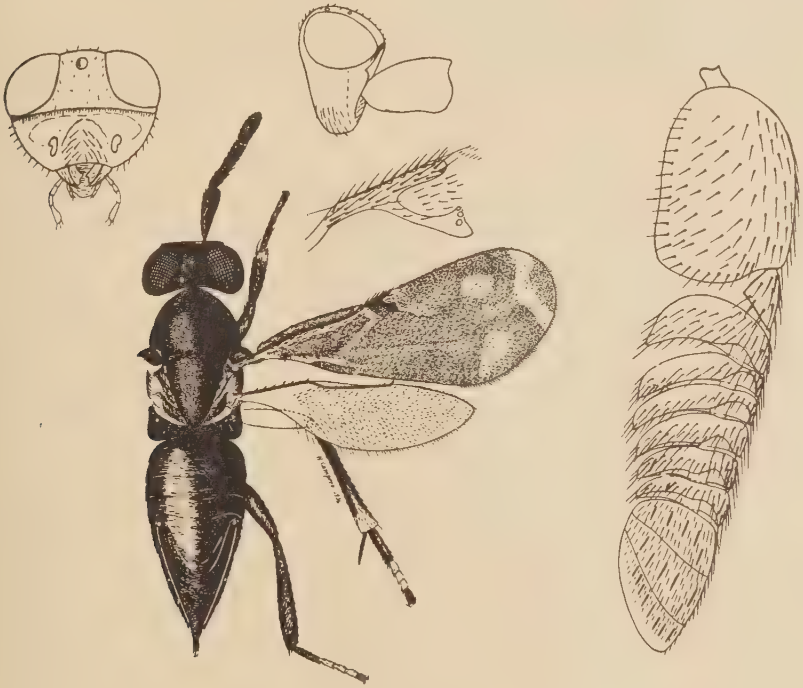

Fig. 3. *Cerapterocerus inutilis*, sp. n. ♀.

Head (dorsal view) slightly concave posteriorly, anteriorly with the narrow frontal ledge visible ; twice as wide as long ; frontovertex finely reticulate punctate, about twice as long as wide (15 : 7) ; at the median ocellus slightly more than one-fourth the head width (7 : 30) ; ocellar triangle acute, almost equilateral ; the median ocellus about its own diameter from the orbits, the posterior pair almost contiguous with the orbits and more than their diameter from the occipital margin. Head (frontal view) wider than high (5 : 4) ; scrobes not differentiated from the concave facial depression, bounded above by a narrow, carinated, transverse ledge. The ledge bluish, highly metallic, and provided with thick, silvery refractive, appressed setae. Upper part of facial impression rounded, finely granularly reticulate punctate, especially towards the sides. A broad median convexity between the antennae with whitish setae towards the mouth. Mesoscutum slightly more than one and one-half times as long as wide (13 : 8). Scutellum elongate, tapering to a narrowed, rounded apex, longer than the mesoscutum (5 : 4) ; provided with sparse, fine, dark setae. Abdomen slender, pointed at the apex, ovipositor shortly exserted.

Other parts as shown in figure 3.

Length, 2·2 mm.

Described from 4 ♀♀, ex *Ceroplastes* sp., Limuru, Kenya, 11.xi.1935, 3.iii.1936.

Silvestri has given an account of the immature stages of *Cerapterocerus mirabilis*, Westwood, as a parasite of *Phaenodiscus aeneus* (Dalm.) within *Sphaerolecanium prunastri* (Fonsc.). The *Cerapterocerus* described in this paper may prove to be an injurious hyperparasite.

Family APHELINIDAE.

Coccophagus isipingoensis, Compere.

Coccophagus isipingoensis, Compere, Proc. U.S. Nat. Mus., 78 (7) : 57–59, 1931.

Nine ♀♀ and one ♂ reared from *Ceroplastes* sp., Uganda, October and December 1935.

Coccophagus amblydon, sp. nov.

A moderately large, dominantly black species, with the apex of the scutellum lemon-yellow and the centre of the forewings faintly but extensively infuscated. This species is most closely related to *C. malthusi*, Girault, and *saintebeauvei*, Girault. It can be separated from the great majority of species by the following diagnostic characters : scutellum about as setose as the mesoscutum, the paired bristles at the apex as long as the scutellum ; abdomen pointed at the apex ; seventh tergite long ; ovipositor shortly exserted ; antennal club subequal in length to the first funicle joint ; first funicle joint three times as long as wide, the sensoria about one-third as long as the segment and extending the entire length in three longitudinal files ; base of middle tibiae with a group of coarse black setae ; outer aspect of hind tibiae with moderately coarse black setae.

♀. Head and body black to dark brown, except the apical one-fourth of the scutellum which is lemon-yellow. Legs dominantly black to dark brown with the following parts sordid white : (One foreleg concealed, the other and the tarsi of the hind legs missing) middle femora towards the apex and a narrow annulus at base ; middle and hind tibiae tipped at basal ends ; tarsi of middle legs. Tibial spur of middle legs blackish. Forewings with a faint but extensive central cloud curving outward beyond the stigma and disappearing near the posterior margin.

Scape slightly longer than the first funicle joint (9 : 7) ; pedicel one and one-half times as long as wide ; less than one-half as long as the first funicle joint ; first funicle joint almost three times as long as wide, the succeeding decreasing in length ; ratio of funicle joint lengths 7–6–5 ; club not much wider than the third funicle joint and subequal in length to the first. Funicle and club with numerous sensoria, those on the club as long as the segments and those on the funicle from one-third to one-half the lengths of the segments.

Marginal vein longer than the submarginal (5 : 4) ; stigmal vein short and wide ; postmarginal vein spur-like, not extending distad beyond the apex of the stigmal vein. Forewings with a narrow, bare area along the posterior margin at base. Hind wings broadly rounded at the apex.

Mandibles almost edentate.

Length, 1·7 mm.

Described from 1 ♀, holotype, ex *Ceroplastes destructor*, Newst., Uganda, 29.xii.1935 (*T. H. C. Taylor*).

After the holotype was examined on a tag, it was boiled in potash, then cleared and mounted in balsam.

So far as known, all the species of *Coccophagus* in the female sex are primary parasites. S. E. Flanders has recently discovered that many species of *Coccophagus*, as well as species of related genera, develop hyperparasitically in the male sex. The fertilised females produce female progeny exclusively, which develop as primary parasites within Coccids. Unfertilised females produce male progeny exclusively, which develop hyperparasitically on or within female larvae of their own species or on or within the larvae of other Chalcidoids that inhabit Coccids.

The way in which the different sexes are produced by *Coccophagus*, *i.e.*, females as primary parasites from mated parents and males as hyperparasites from unmated parents, is an important discovery that should not be overlooked when attempts are made to establish *Coccophagus* species in new habitats. In the past, many attempts to propagate *Coccophagus* species for introduction into new habitats were unsuccessful because of a lack of knowledge regarding this phenomenon.

Family MISCOGASTERIDAE.

Scutellista sp.

In the specimens of *Scutellista* from Kenya, which inhabit wax scales, the apical margins of the forewings appear narrowly bare after being mounted in balsam. In *Scutellista cyanea* (Motsch), as represented by specimens from *Saissetia oleae* (Bern.), the forewings appear ciliated to the apical margin. The bare appearance towards the apex of the forewings in the Kenya samples is the effect produced by cilia which become transparent in balsam. Aside from this rather trivial difference, the two forms appear similar.

The observations of the Entomological Branch in New South Wales seem to show that at least two biological forms of *Scutellista* are classified under the name *cyanea*. In the practical work of biological control it is fundamentally necessary to recognise the forms which have distinct capacities, regardless of whether or not taxonomists are able to differentiate between them on the basis of adult morphology. Eventually it may be found more practical to give these forms a varietal name than to use the term " wax scale inhabiting *Scutellista cyanea* from Kenya."

THE MECHANISM OF RESPIRATION OF LOCUSTS AND ITS BEARING ON THE PROBLEM OF INHALATION OF POISON DUSTS.

By A. G. Hamilton, B.Sc., B.Agr., Ph.D., D.I.C.

Introduction.

The recent field experiments (King, 1934) on the destruction of locusts in flight by means of a poison dust (sodium arsenite) delivered from aircraft, while suggesting the possibility of poisoning locusts in the air, provided no conclusive data on the physiological mode of action of poison dust applied externally. This action was previously thought (King & Ruttledge, 1932) to be due to the inhalation of poison dust, and it was argued that the toxic effects should be accelerated in the flying locusts owing to their higher rate of respiration as compared with resting individuals.

An elucidation of the mode of action of external poisons applied in the form of dust would obviously have no mere academic interest, since this knowledge is essential in the selection of a poison to replace sodium arsenite. This was considered highly desirable by two successive International Locust Conferences (London, 1934, and Cairo, 1936).

It was with this aim that the experiments described in the present paper were carried out in the Locust Laboratory of the Imperial Institute of Entomology, British Museum (Natural History), and in the Entomology Department of the Royal College of Science, London, with financial assistance from Imperial Chemical Industries, Ltd.

The object of the experiments was to obtain direct evidence whether poison dusts kill locusts by entering the respiratory system, and if so what is the size of particles capable of passing the spiracular openings. The work included, therefore, measurements of the latter, and experiments in dusting, with subsequent examination of tracheal trunks arising from all spiracles for the presence of particles of dust. This would indicate which spiracles serve for inspiratory action and which, therefore, had to be examined in further experiments designed to test the effects of the length of exposure on the amount of dust of different grades present in the tracheae.

Apparatus and Methods.

All the locusts used in these experiments were bred in cages under optimum conditions of humidity and temperature (Hamilton, 1936).

The measurements of the spiracles and the tracheae were made under a binocular and a microscope fitted with a micrometer scale. These measurements are given both in millimetres and inches so as to make them comparable with meshes of British Standard Sieves, which are given in inches.

The examination of the tracheae for the presence of dust was also made under the binoculars and microscope after the locusts had been dusted for varying periods with different grades (150 to 300 B.S.S.) of cuprous cyanide. The reasons for using cuprous cyanide were: (1) it is insoluble and therefore remained in the tracheae; (2) if the locusts were killed in H_2S gas this converted the cuprous cyanide into copper sulphide, which is black and thus easily observed in the white tracheae. In order to prove that the black particles of dust seen in the tracheae were cuprous sulphide, colour tests for copper were made, using the sodium diethyl dithiocarbamate method.

The dusting of the locusts was carried out in the wind tunnel (fig. 1) at a constant temperature of 90°F. (32·3°C.). This tunnel, as may be seen from the figure, was built inside a large glass cage (A) where the temperature was regulated by a thermostat (B) which controlled the heater (C). The locusts (always two used in each experiment) were suspended by cotton thread from points D and E. In the case of the experiments on flying locusts the thread was tied between the first and second pair of legs and then over the pronotum or between the anterior and posterior pairs of

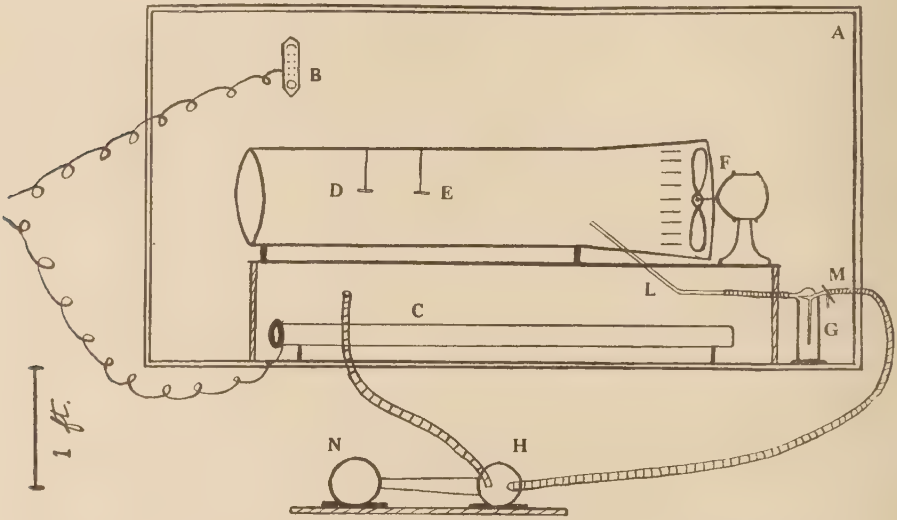

Fig. 1. Diagrammatic section of the wind tunnel: A, cage surrounding wind tunnel; B, thermostat; C, electric heater; D, E, positions where locusts were suspended when dusted; F, fan; G, dust-blower; H, rotary pump; L, tube connecting dust-blower with tunnel; M, two-way tap; N, electric motor.

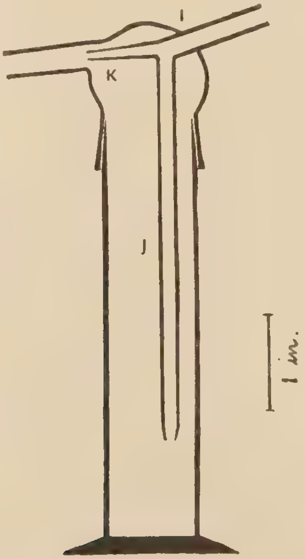

Fig. 2. Diagrammatic section of the dust-blower: I, air inlet into blower; J, K, air tubes in blower.

wings. The latter position seemed to cause less dragging in heavy females. Also it did not interfere with the first pair of spiracular openings in the case of locusts which had the side projection of the pronotum removed. The fan (F) was then started, and this produced a flow of air along the tunnel at approximately 5 miles an hour, to which locusts responded by flying. When the locusts were flying steadily in the stream of air, dust was blown into the tunnel from the dust-blower (G) (also fig. 2) for a given period. The dust-blower was worked by air sucked out of the cage at the required temperature and pumped by the rotary pump (H), at a pressure of 10·5 mm. mercury, into it at I (fig. 2). On entering the blower, the stream of air was divided, one stream passing down the tube J and stirring up the dust at the bottom, the other stream passing along K thus helping to suck the dust out of the blower. The dust passes along the tubing L (fig. 1) and enters the tunnel as a cloud. At M there is a two-way tap, so that the exposure of the locusts to the cloud of dust could be controlled to within a second. This was found to be the most suitable method, because it was possible to have the locusts flying before exposing them to the cloud of dust. The importance of this will be seen later when describing the results of dusting flying and non-flying locusts (see p. 64).

In the experiments where adult locusts were not allowed to fly, all four wings were tied together and suspended by the thread in the tunnel. Similarly, 5th instar hoppers were suspended by the wing buds. The air in the tunnel was still and the dust blown in by the blower as in the other experiments ; the fan only being used to blow away the dust at the end of the exposure.

Position of the Spiracles.

There are ten pairs of spiracles in locusts, two pairs on the thorax and eight pairs on the abdomen. The position of the spiracles is as follows on each side :—the first is situated on the membrane connecting the prothorax and the mesothorax and is covered by the projecting lateral margin of the pronotum. It is larger (as will be seen later) than the others and connects with two main tracheal tubes. The second is quite exposed, being situated above the coxal cavity of the middle leg. Both the first and second spiracles are closed externally by a two-lobed valve. The third (first abdominal) spiracle is situated in the tympanal organ, close to the front margin. The remaining seven abdominal spiracles are situated on the tergites of segments 2 to 9 of the abdomen. All the abdominal spiracles have the closing apparatus at the inner end of the atrium cavity.

Measurements of the Spiracles and Tracheae.

1. *Locusta migratoria migratorioides*, R. & F.

The measurements of the spiracles and tracheae of adults and fifth instar hoppers of this species are given in Tables I and II. In the case of the first and second pairs of spiracles it is only possible to give the length of the opening, as the outer valves of the atrium always close when the locust is killed. In the abdominal spiracles, where the closing apparatus is situated at the inner end of the atrium cavity, it is always possible to measure the width of the opening to the atrium but this unfortunately does not mean that this is the size of the opening to the tracheae. If these measurements are compared with those in Table III, which gives the size of the opening in the different grades of British Standard Sieves and hence the size of the largest particles of dust which pass these sieves, it may be seen that it should be possible for these smallest particles to enter all the tracheae. The finest dust used in the experiments had passed a 300 B.S. sieve and therefore contained particles of dust smaller than the size of the openings in the sieve and which should be capable of passing through the smallest spiracular opening.

2. *Schistocerca gregaria*, Forsk.

Only the spiracles and tracheae of adults of this species were measured. It may be seen from Table IV that the size is approximately the same as for *Locusta* adults, and they are also large enough to allow some of the finest dust to enter.

TABLE I.

Measurements of Spiracles and Tracheae of Adults of Locusta.

Spiracle No.	Average length of spiracle		Average width of spiracle		Diameter of tracheae connecting spiracle	
	ins.	mm.	ins.	mm.	ins.	mm.
			Males.			
1	·0320	·813	—	—	·0257 ·0183	·653 ·465
2	·0220	·559	—	—	·0179	·455
3	·0118	·300	·0069	·175	·0177	·450
4	·0124	·315	·0065	·165	·0178	·452
5	·0085	·215	·0049	·124	·0135	·343
6	·0068	·173	·0035	·088	·0111	·282
7	·0060	·153	·0032	·081	·0102	·259
8	·0056	·142	·0025	·064	·0102	·259
9	·0057	·145	·0030	·076	·0094	·238
10	·0105	·268	·0057	·145	·0175	·445
			Females.			
1	·0390	·991	—	—	·0237 ·0130	·602 ·330
2	·0290	·737	—	—	·0225	·572
3	·0148	·376	·0070	·178	·0253	·643
4	·0143	·363	·0070	·178	·0177	·450
5	·0095	·241	·0047	·119	·0168	·427
6	·0083	·211	·0038	·097	·0166	·422
7	·0070	·178	·0029	·074	·0166	·422
8	·0070	·178	·0027	·069	·0132	·335
9	·0075	·191	·0028	·071	·0166	·422
10	·0126	·320	·0064	·162	·0228	·579

TABLE II.

Measurements of Spiracles and Tracheae of 5th Hoppers of Locusta.

Spiracle No.	Average length of spiracle ins.	mm.	Average width of spiracle ins.	mm.	Diameter of tracheae connecting spiracle ins.	mm.
			Males.			
1	·0330	·838	—	—	·0225 ·0150	·572 ·381
2	·0200	·508	—	—	·0195	·495
3	·0105	·267	·0060	·152	·0150	·381
4	·0100	·254	·0060	·152	·0125	·292
5	·0065	·165	·0033	·084	·0125	·292
6	·0055	·140	·0030	·076	·0125	·292
7	·0048	·123	·0030	·076	·0115	·292
8	·0045	·114	·0030	·076	·0107	·272
9	·0048	·123	·0033	·084	·0107	·272
10	·0090	·229	·0052	·132	·0133	·338
			Females.			
1	·0330	·838	—	—	·0250 ·0150	·635 ·381
2	·0255	·648	—	—	·0240	·610
3	·0098	·249	·0060	·152	·0190	·482
4	·0095	·241	·0045	·114	·0190	·482
5	·0085	·216	·0040	·102	·0180	·457
6	·0068	·173	·0035	·089	·0135	·342
7	·0050	·127	·0025	·064	·0135	·342
8	·0055	·140	·0025	·064	·0135	·342
9	·0055	·140	·0030	·076	·1305	·342
10	·0105	·267	·0055	·140	·0180	·457

TABLE III.

Size of Aperture and Diameter of Wire in British Standard Sieves, as supplied by Imperial Chemical Industries Ltd.

Mesh	Aperture (side of square) ins.	mm.	Diameter of wire ins.	mm.
300	·0021	·053	·0012	·030
240	·0026	·066	·0016	·041
200	·0030	·076	·0020	·051
150	·0041	·104	·0026	·066

TABLE IV.

Measurements of Spiracles and Tracheae of Adults of Schistocerca.

Spiracle No.	Average length of spiracle		Average width of spiracle		Diameter of tracheae connecting spiracle	
	ins.	mm.	ins.	mm.	ins.	mm
			Males.			
1	·0270	·940	—	—	·0235 ·0200	·596 ·508
2	·0280	·711	—	—	·0230	·584
3	·0155	·394	·0095	·241	·0190	·483
4	·0125	·317	·0060	·152	·0175	·445
5	·0090	·229	·0055	·140	·0140	·356
6	·0065	·165	·0035	·089	·0120	·305
7	·0060	·152	·0030	·076	·0115	·292
8	·0060	·152	·0030	·076	·0110	·279
9	·0060	·152	·0035	·089	·0110	·279
10	·0110	·279	·0060	·152	·0170	·432
			Females.			
1	·0385	·978	—	—	·0250 ·0195	·635 ·495
2	·0265	·673	—	—	·0185	·470
3	·0175	·445	·0100	·254	·0185	·470
4	·0155	·394	·0075	·191	·0175	·445
5	·0080	·203	·0055	·140	·0150	·384
6	·0070	·179	·0050	·127	·0140	·356
7	·0060	·152	·0045	·114	·0120	·305
8	·0060	·152	·0045	·114	·0120	·305
9	·0060	·152	·0040	·102	·0160	·407
10	·0115	·292	·0075	·191	·0200	·508

Function of each Spiracle.

As Lee (1925) and Snodgrass (1929 and 1935) have gone fully into the respiratory movements of grasshoppers and the muscles connected with such movements, it is only necessary to consider, for the purpose of the present paper, the actual part played by the different spiracles during respiration.

The old view, and one still held by MacKay (1927), is that each spiracle is both inspiratory and expiratory in function. MacKay working on grasshoppers found, by immersing different parts of the grasshopper in water, that inspiration could be through the anterior group ot spiracles and expiration through the posterior group or *vice versa*. Du Buisson (1924) working on two species of *Chorthippus* (*Stenobothrus*) says the thoracic spiracles function for both expiration and inspiration, while the abdominal only function for inspiration. Lee (1925, 1927 and 1927a), who experimented on a very large number of species (*Melanoplus femur-rubrum*, DeGeer, *M. differentialis*, Thomas, *M. bivitattus*, Say, *M. atlantis*, Riley, *M. viridipes*, Scudder, *Schistocerca americana*, Drury, *Dissosteira carolina*, Lin., *Spharagemon bolli*, Scudder, *Chortophaga viridifasciata*, DeGeer, *Mecostethus lineatus*, Scudder, and *Hippiscus tuberculatus*, P. Beauv.), came to the conclusion that the first four spiracles are for inspiration and the last six for expiration. This opinion has been more recently put forward by Fraenkel (1932) for *Schistocerca gregaria*, Forsk., as the usual method of respiration, but he also suggests the possibility of the posterior six having an inspiratory function as well. McArthur (1929), working on *Romalea microptera* var. *marci*, Loding, *Schistocerca obscura*, Fabr., *S. americana*, Drury, and *Melanoplus differentialis*, Thomas, and using the methods of Lee and MacKay, attempted to test the conflicting results obtained by these two workers. His results confirm those of Lee, that the usual course of air currents is inwards through the first four spiracles and outwards through the last six, but they also partly support MacKay's results in so far that he found that the first four spiracles are capable of acting both for inspiration and expiration of air. This double action of the first four spiracles he attributed to the fact that the internal mechanism is capable of changing the times of opening and closing of the spiracular valves in relation to the expansion and contraction of the body.

In my experiments (see Tables V–X), I have investigated the possibility of spiracles acting differently when the locusts are flying or motionless, and so far as the last pair of spiracles is concerned this has proved to be the case. My conclusions as to which spiracles act for inspiration are based on the presence or absence of particles of dust. This method unfortunately only proves that a certain spiracle has an inspiratory function if particles of dust are present, but the presence of dust does not rule out the possibility of this particular spiracle also having an expiratory function, the two functions alternating very quickly. On the other hand the absence of dust does, to a very large extent, prove that the spiracle is only expiratory in function.

In Tables V–VII for *Locusta* adults and VIII–X for *Schistocerca* adults, it is definitely shown that the 2nd, 3rd and 4th spiracles, under all conditions, have an inspiratory function, as there was not a single experiment (exposure 30 seconds) when dust was not found in these spiracles. In the case of the first spiracle the results, though not so definite, also show that this spiracle always has an inspiratory function. In order to demonstrate this it was necessary to remove the posterior projection of the pronotum, as the spiracle is normally behind this and the dust does not reach it (as this is purely a chitinous projection, its removal causes no inconvenience to the locust). When the projection was removed dust was found to be present in 81 per cent. of the *Locusta* and 100 per cent. of the *Schistocerca* specimens examined ; the exceptions being in specimens No. 4 (Table V), No. 4 (Table VI), when no dust was present, and Nos. 3, 6, 12, 16, 18 and 26 (Table V), No. 6 (Table VI) and No. 5 (Table VII), when the results were doubtful. Doubtful implies that one or two particles of dust were present, but as this might be due to accident it is regarded as not sufficient to prove either the presence or absence of dust.

Now passing to the 5th, 6th, 7th, 8th and 9th spiracles, there is absolutely no doubt as to their function in both species. This is purely expiratory, as in no specimen were particles of dust ever found in the tracheae connecting these spiracles.

The most interesting results were obtained with the 10th spiracle, which is capable of functioning either as expiratory or inspiratory, according to whether the locust is flying or motionless. When flying locusts were exposed to a cloud of dust for 30 seconds the last spiracle very seldom contained any dust. It may be seen (Table V) that 54 out of 58 (93·1 per cent.) of the *Locusta* definitely contained no dust, and of the other four, two (No. 9) contained dust and two (Nos. 11 and 17) were doubtful cases. In Table VIII for *Schistocerca*, 8 out of 10 contained no dust and of the others one (No. 2) did and one (No. 5) was doubtful. The results of the penetration

TABLE V.

Showing the Spiracles through which Dust entered when flying Adults of Locusta *were exposed for* 30 *seconds to a Cloud of fine Dust; the Projection on one side of the Pronotum having been removed.*

No.	Side of pronotum with projection removed	Side of locust from which the tracheae were examined	Spiracle									
			1	2	3	4	5	6	7	8	9	10
Males.												
1	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
2	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
3	Left	Left	D	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
4	Left	Left	—	P	P	P	—		—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
5	Left	Left	P†	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
6	Left	Left	D	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
7	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
8	Left	Left	P†	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—		—	—	—	—
9	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—		—	—	—	P
10	Right	Left	—	P	P	P	—	—	—	—	—	—
		Right	P*	P	P	P	—	—	—	—	—	—
11	Right	Left	—	P	P	P	—	—	—	—	—	D
		Right	P*	P	P	P	—	—	—	—	—	—
12	Right	Left	—	P	P	P	—	—	—	—	—	—
		Right	D*	P	P	P	—	—	—	—	—	—
13	Left	Left	P†	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
14	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
Females.												
15	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
16	Left	Left	D	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
17	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	D
18	Left	Left	D	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
19	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
20	Left	Left	P†	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
21	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
22	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
23	Left	Left	P†	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
24	Right	Left	—	P	P	P	—	—	—	—	—	—
		Right	P†	P	P	P	—	—	—	—	—	—
25	Right	Left	—	P	P	P	—	—	—	—	—	—
		Right	P*	P	P	P	—	—	—	—	—	—
26	Right	Left	—	P	P	P	—	—	—	—	—	—
		Right	D	P	P	P	—	—	—	—	—	—
27	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
28	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
29	Left	Left	P†	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—

P indicates that dust was present.
D ,, only one or two particles observed, therefore rather doubtful.
— ,, no dust in tracheae.
* ,, in upper branch of tracheae.
† ,, in both upper and lower branches of tracheae.

of particles of dust into the tracheae of non-flying locusts, exposed to a cloud of dust for 30 seconds, were contrary to what was found with flying locusts. In the case of *Locusta* (Table VI) 12 out of 20 (60 per cent.) contained particles of dust, 5 were doubtful and in only 3 was there definitely no dust. Only 4 *Schistocerca* were examined, and these all contained particles of dust. Now passing to those individuals which were dusted when flying, but stopped flying for a second or so during the experiment, it will be seen (Table VII for *Locusta* and Table X for *Schistocerca*) that in the majority of the tracheae connecting the 10th spiracle particles of dust were present. This shows that short cessation in flight causes an alteration in the function of the 10th spiracle.

If a comparison is made between the size and number of branches of the tracheae connecting spiracle 10 with those connecting spiracles 5–9, further support of the function of this spiracle being inspiratory is obtained. No detailed study of this has been made, but it is obvious from the few measurements given that they are comparable in size with those connecting spiracles 1–4, which have been proved to be always inspiratory in function, whereas those connecting spiracles 5–9, are always expiratory in function and only about half the size.

Only a few experiments have been carried out on 5th instar hoppers, because these showed that respiration is the same as in non-flying adults.

TABLE VI.

Showing the Spiracles through which Dust entered when non-flying Adults of Locusta *were exposed for* 30 *seconds to a Cloud of fine Dust, the Projection on one side of the Pronotum having been removed.*

No.	Side of pronotum with projection removed	Side of locust from which the tracheae were examined	Spiracle									
			1	2	3	4	5	6	7	8	9	10
Males.												
1	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
2	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
3	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
4	Left	Left	—	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	D
5	Left	Left	P*	P	P	P	—	—	—	—	—	D
		Right	—	P	P	P	—	—	—	—	—	—
Females.												
6	Left	Left	D	P	P	P	—	—	—	—	—	D
		Right	—	P	P	P	—	—	—	—	—	—
7	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	D
8	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
9	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
10	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P

P indicates that dust was present.
D ,, only one or two particles observed, therefore rather doubtful.
— ,, no dust in tracheae.
* ,, in upper branch of tracheae.

TABLE VII.

Showing the Spiracles through which Dust entered when flying Adults of Locusta *were exposed for* 30 *seconds to a Cloud of fine Dust, but were stopped flying for a few seconds, the Projection on one side of the Pronotum having been removed.*

No.	Side of pronotum with projection removed	Side of locust from which the tracheae were examined	Spiracle									
			1	2	3	4	5	6	7	8	9	10
Males.												
1	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
2	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
3	Left	Left	P†	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	P
4	Left	Left	P†	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	D
Females.												
5	Left	Left	D	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
6	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
7	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	—

P indicates that dust was present.
D ,, only one or two particles observed, therefore rather doubtful.
— ,, no dust in tracheae.
* ,, in upper branch of tracheae.
† ,, in both upper and lower branches of tracheae.

TABLE VIII.

Showing the Spiracles through which Dust entered when flying Adults of Schistocerca *were exposed for* 30 *seconds to a Cloud of fine Dust, the Projection on one side of the Pronotum having been removed.*

No.	Side of pronotum with projection removed	Side of locust from which the tracheae were examined	Spiracle									
			1	2	3	4	5	6	7	8	9	10
Males.												
1	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
2	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	P
3	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
Females.												
4	Left	Left	P*	P	P	P	—	—	—	—	—	—
		Right	—	P	P	P	—	—	—	—	—	—
5	Left	Left	P*	P	P	P	—	—	—	—	—	D
		Right	—	P	P	P	—	—	—	—	—	—

P indicates that dust was present.
D ,, only one or two particles observed, therefore rather doubtful.
— ,, no dust in tracheae.
* ,, in upper branch of tracheae.

TABLE IX.

Showing the Spiracles through which Dust entered when non-flying Adults of Schistocerca *were exposed for* 30 *seconds to a Cloud of fine Dust the Projection on one side of the Pronotum having been removed.*

No.	Side of pronotum with projection removed	Side of locust from which the tracheae were examined	Spiracle									
			1	2	3	4	5	6	7	8	9	10
Males.												
1	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P
Females.												
2	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P

P indicates that dust was present.
— ,, no dust in tracheae.
* ,, in upper branch of tracheae.

TABLE X.

Showing the Spiracles through which Dust entered when a flying Adult of Schistocera *was exposed for* 30 *seconds to a Cloud of fine Dust, but stopped flying for a few seconds the Projection on one side of the Pronotum having been removed.*

No.	Side of pronotum with projection removed	Side of locust from which the tracheae were examined	Spiracle									
			1	2	3	4	5	6	7	8	9	10
1	Left	Left	P*	P	P	P	—	—	—	—	—	P
		Right	—	P	P	P	—	—	—	—	—	P

P indicates that dust was present.
— ,, no dust in tracheae.
* ,, in upper branch of tracheae.

Discussion on Respiration.

My results, given above, agree with those of Lee (1925) and Fraenkel (1932) with regard to the function of the first four spiracles. I have shown that this function is inspiratory under all conditions, but as I have not attempted to find if there is an expiratory function going on at the same time, I can neither agree nor disagree with the findings of Du Buisson (1924), MacKay (1927) or McArthur (1929), who are of the opinion that they have a double function. My results on the last six spiracles are more definite, because particles of dust were never found in the 5th, 6th, 7th, 8th or 9th, and found only in the 10th in non-flying individuals. This means that spiracles 5 to 9 never function as inspiratory, which is in agreement with Lee but contrary to MacKay and Du Buisson, also partly contrary to Fraenkel, as he says these spiracles may sometimes function as inspiratory as well as expiratory. It is in the experiments on the 10th spiracle, which in flying locusts functions as expiratory only and in non-flying locusts as inspiratory and which may or may not function as expiratory at the same time, that my results are contrary to those of Lee but agree with those of MacKay and Du Buisson. As I have not proved or disproved the expiratory function at the same time as the inspiratory, I cannot agree or disagree with Fraenkel, who thinks it also may have a double function.

The contradictory results of these various workers may be partly due to the fact that different species have, to a large extent, different respiratory movements, or to the individual used in the experiments being capable of altering these movements. That the latter and not the former is the more likely reason may be concluded from the fact that several workers experimented on the same species. Although all these workers used resting individuals, their experiments were carried out under such unnatural conditions that there is every reason to suggest that the individuals might have changed their respiratory movements according to the muscles they were exerting in order to free themselves. This is supported by my experiments carried out under as natural conditions as it is possible to produce. I found that spiracles 1 to 4 always function as inspiratory and spiracles 5 to 9 as expiratory, while spiracle 10 functions as expiratory when the locust is flying and inspiratory when the locust is resting.

The Effect of the Length of Exposure on the Amount of different Grades of Dust present in the Tracheae.

1. *Presence of Particles of Dust.*

Only locusts which were dusted with cuprous cyanide when flying in the wind tunnel and then killed with hydrogen sulphide are included in these results. The length of exposure varied from 10 to 30 seconds and the grades of dust from 300 to 150 British Standard Sieve. The tracheae examined were those connecting spiracles 2, 3 and 4, because these have been shown to give the most constant results and always function as inspiratory. Also the measurements given above (p. 57) demonstrate that particles of dust which have passed even through a 150 British Standard Sieve would be able to enter these spiracles.

The method of killing the locusts with hydrogen sulphide gas after dusting was found to be rather important. If they were killed very quickly in a concentrated atmosphere of the gas the spiracles closed immediately and did not permit sufficient hydrogen sulphide to enter and react with the cuprous cyanide, whereas if killed in a less concentrated atmosphere the gas was circulated through the tracheae by the respiratory movements and had time to react with the cuprous cyanide and convert it into copper sulphide.

In the results obtained it has been impossible to give exact measurements of the amount of dust present, but rough estimates showing the effect of the length of exposure on the amount of dust have been made as follows :—(1) no dust present in the tracheae ; (2) presence of dust doubtful, when only one or two particles observed and these might have entered by accident ; (3) only a few particles present ; (4) 10 per cent. of walls of tracheae immediately inside the spiracles covered with particles of dust ; (5) 20 per cent. or more of walls immediately inside the spiracles covered with particles of dust.

In the results, Tables XI–XIII, it is shown that the length of exposure is very important if inhalation of dust is to be effective. This is applicable to all grades of dust experimented with but more especially in the case of the coarser dust (150 B.S.S.). It may be seen from these tables that in the case of 10 seconds exposure there was only one trachea which did not contain dust when the locust was dusted with 300 B.S.S. cuprous cyanide, and all contained dust when 200 B.S.S. was used, but with the coarser dust (150 B.S.S.) as many as three tracheae connecting the 2nd and 3rd spiracles and four connecting the 4th spiracle contained no dust. The maximum amount of dust in any tracheae with this length of exposure never exceeded a few particles. When the exposure was increased to 20 seconds the amount of dust increased in every case, and in some cases 10 per cent. of the walls of the tracheae was covered with dust. There was only one trachea (with 200 B.S.S.) where no dust was present. Also the percentage of spiracles where the presence of dust was doubtful was greatly reduced. With a further increase in the time of exposure to 30 seconds the amount of dust present increased, and in many cases, especially with the 300 and

200 B.S.S., 20 per cent. of the walls was covered with dust. There were no tracheae where there was no dust or where its presence was doubtful.

TABLE XI.

Showing the Effect of Dusting flying Adults of Locusta *with* 300 *B.S.S. Cuprous Cyanide Dust for different Lengths of Exposure ; Males and Females given together as no significant difference was found.*

Tracheae connecting spiracle number	No. of tracheae examined	Percentage of tracheae in which different amounts of dust were present ; the actual figures given in brackets				
		No dust present	Presence of of dust doubtful	Only a few particles of dust present	10 per cent. of walls of tracheae covered with dust	20 per cent. or more of walls of tracheae covered with dust
			10 *Seconds*	*Exposure*		
2	24	0 (0)	16·7 (4)	83·3 (20)	0 (0)	0 (0)
3	,,	4·2 (1)	20·8 (5)	75·0 (18)	0 (0)	0 (0)
4	,,	0 (0)	25·0 (6)	75·0 (18)	0 (0)	0 (0)
			20 *Seconds*	*Exposure.*		
2	40	0 (0)	0 (0)	72·5 (29)	22·5 (9)	5·0 (2)
3	,,	0 (0)	0 (0)	80·0 (28)	30·0 (12)	0 (0)
4	,,	0 (0)	10·0 (4)	80·0 (32)	7·5 (3)	2·5 (1)
			30 *Seconds*	*Exposure*		
2	80	0 (0)	0 (0)	21·5 (17)	55·0 (44)	23·5 (19)
3	,,	0 (0)	0 (0)	22·5 (18)	46·7 (39)	28·8 (23)
4	,,	0 (0)	0 (0)	60·0 (48)	40·0 (32)	0 (0)

TABLE XII.

Showing the Effect of Dusting flying Adults of Locusta *with* 200 *B.S.S. Cuprous Cyanide Dust for different Lengths of Exposure ; Males and Females given together as no significant difference was found.*

Tracheae connecting spiracle number	No. of tracheae examined	Percentage of tracheae in which different amounts of dust were present ; the actual figures given in brackets				
		No dust present	Presence of of dust doubtful	Only a few particles of dust present	10 per cent. of walls of tracheae covered with dust	20 per cent. or more of walls of tracheae covered with dust
			10 *Seconds*	*Exposure.*		
2	24	0 (0)	45·8 (11)	54·2 (13)	0 (0)	0 (0)
3	,,	0 (0)	16·7 (4)	83·3 (20)	0 (0)	0 (0)
4	,,	0 (0)	58·3 (14)	41·7 (10)	0 (0)	0 (0)
			20 *Seconds*	*Exposure*		
2	32	0 (0)	0 (0)	65·6 (21)	34·4 (11)	0 (0)
3	,,	0 (0)	0 (0)	56·3 (18)	43·7 (14)	0 (0)
4	,,	3·1 (1)	12·5 (4)	81·3 (26)	3·1 (1)	0 (0)
			30 *Seconds*	*Exposure*		
2	28	0 (0)	0 (0)	35·7 (10)	39·3 (11)	25·0 (7)
3	,,	0 (0)	0 (0)	32·1 (9)	32·1 (9)	35·7 (10)
4	,,	0 (0)	0 (0)	50·0 (14)	42·8 (12)	7·1 (2)

TABLE XIII.

Showing the Effect of Dusting flying Adults of Locusta *with* 150 *B.S.S. Cuprous Cyanide Dust for different Lengths of Exposure; Males and Females given together as no significant difference was found.*

Tracheae connecting spiracle number	No. of tracheae examined	Percentage of tracheae in which different amounts of dust were present; the actual figures given in brackets				
		No dust present	Presence of of dust doubtful	Only a few particles of dust present	10 per cent. of walls of tracheae covered with dust	20 per cent. or more of walls of tracheae covered with dust
			10 *Seconds*	*Exposure*		
2	16	18·8 (3)	36·2 (6)	45·0 (7)	0 (0)	0 (0)
3	,,	18·8 (3)	25·0 (4)	56·2 (9)	0 (0)	0 (0)
4	,,	25·0 (4)	45·0 (7)	30·0 (5)	0 (0)	0 (0)
			20 *Seconds*	*Exposure*		
2	20	0 (0)	5·0 (1)	95·0 (19)	0 (0)	0 (0)
3	,,	0 (0)	0 (0)	50·0 (10)	50·0 (10)	0 (0)
4	,,	0 (0)	15·0 (3)	80·0 (16)	5·0 (1)	0 (0)
			30 *Seconds*	*Exposure*		
2	12	0 (0)	0 (0)	50·0 (6)	41·7 (5)	8·3 (1)
3	,,	0 (0)	0 (0)	25·0 (3)	50·0 (6)	25·0 (3)
4	,,	0 (0)	0 (0)	75·0 (9)	25·0 (3)	0 (0)

2. *Chemical Tests for Copper.*

In order to prove conclusively that the black particles seen in the tracheae were particles of copper sulphide, chemical tests were made. The tracheae were removed from the locusts which had been dusted for different lengths of exposure with 300 B.S.S. and tested. They were boiled for a few minutes in dilute nitric acid. The solution was then made slightly ammoniacal and a few drops of 0·01 per cent. solution of sodium diethyl dithiocarbamate were added which in the presence of copper produce a yellow colour.

The number of tests made and the results are given in Table XIV, where it may be seen that the length of exposure is very important. With 10 seconds exposure only a trace of yellow colour was produced in most cases, with 20 seconds exposure slight yellow and yellow were produced, while with 30 seconds exposure a marked yellow colour was produced in three out of four experiments.

TABLE XIV.

Showing different Colour Reactions with Sodium Diethyl Dithiocarbamate according to the Length of Exposure to Dust.

Length of exposure in seconds	No. of locusts examined	Reaction produced			
		Trace of yellow	Slight yellow	Yellow	Marked yellow
10	5	4	—	1	—
20	10	—	4	5	1
30	4	—	1	—	3

Discussion on the probable Mode of Action of Poison Dust.

The results obtained from the dusting experiments in this section of the present paper show that dust which passed a 150 British Standard Sieve, or of a finer grade, is capable of entering the tracheae connecting spiracles 2, 3 or 4, the quantity increasing with the time of exposure. These findings at first tend to support the idea of King & Ruttledge (1932) and King (1934) that locusts are killed by sodium arsenite dust through the respiratory system. However, if the quantity of dust present after a 10 seconds exposure, which is generally regarded as the time required by a locust to fly through a cloud of dust in the field, is considered, it will be seen that the chances of the locust being poisoned in this way are very small. Also the amount of dust in the tracheae is infinitesimal as compared with the amount which accumulates on the exterior of the locust. King & Ruttledge put forward as proof of sodium arsenite poisoning through the spiracles a number of experiments where the dust was applied externally to the various parts of the locust without causing any effect within two days. This non-effectiveness of poison when applied externally is entirely contrary to my results (to be published later) on the external application of various substances (including sodium arsenite), many of which have been found to cause either temporary paralysis or death of the locust. Whether the poison when applied externally penetrates the chitin or acts as a nervous poison through the nerve endings, which are widely distributed over the body of the locust, remains to be studied. Indeed, it is highly probable that the poison may act in both these ways. When a locust is dusted a very considerable quantity of dust collects, even after a short exposure to a cloud of dust, underneath the posterior projection of the pronotum and in other crevices of the body where the chitinous integument is rather thin. It is just as probable that poison would penetrate these membranous parts as the walls of the tracheae, which are ectodermal in origin and therefore of a chitinous nature. If the poison is unable to penetrate the chitin, it will have to reach the end-cells of the tracheae, which is most unlikely. That some poisons act through the nerve endings, alone or in addition to penetration of the external integument, is suggested by the almost immediate occurrence of paralysis when such poisons are applied externally. This paralysis may or may not be followed by the death of the locust, but its symptoms are exactly similar to those that have been reported in the case of a locust swarm passing through a cloud of arsenite dust (King, 1934).

Summary.

1. Measurements of the spiracles and the tracheae of 5th instar hoppers and adults of *Locusta* and adults of *Schistocerca* have been made (see Tables I, II and IV). These measurements show that particles of dust which had passed a 300 B.S. Sieve (*i.e.*, under 0·053 mm. in diameter) are small enough to enter all the spiracles and that the particles which had passed a 150 B.S. Sieve (*i.e.*, under 0·104 mm. in diameter) could enter spiracles 1 to 4 and 10.

2. It has been proved by the presence of particles of dust in the respective spiracles, that spiracles 1 to 4 are inspiratory in function and spiracles 5 to 9 expiratory under all conditions, while the function of spiracle 10 is expiratory when the locust is flying and inspiratory when it is motionless.

3. The quantity of dust present in the tracheae increases with the length of exposure to the cloud of dust ; the quantity present after 10 seconds exposure is not regarded as sufficient to kill the locust.

4. The action of external poisons is thought to be by direct penetration of the integument or through the nerve endings or both.

5. The results given in this paper suggest that further work on the action of poison dusts should be concentrated on the investigation of direct penetration of the integument and of the nerve action, rather than poisoning through the respiratory system.

Acknowledgments.

I wish to express my indebtedness to Dr. B. P. Uvarov, Imperial Institute of Entomology, and Professor J. W. Munro, Royal College of Science, London, for their advice and valuable criticism, to Dr. J. Ferguson, Imperial Chemical Industries, Ltd., for advice on the properties of chemicals and their reactions.

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A NEW ANOPHELES AND A NEW GOELDIA FROM COLOMBIA (DIPT. CULIC.).*

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In 1935 during entomological investigations related to an outbreak of jungle yellow fever in Restrepo, Colombia, I captured a female Anopheline which shows morphological details justifying its description as belonging to a new species of a new subgenus. I also found specimens of a new species of *Goeldia*. These two species are described in the following pages.

Anopheles (Lophopodomyia, n. subgen.) **squamifemur,** sp. n.

Female.—Size about 3·5 mm. Proboscis moderate (1·5 mm.), slender, black. Palpi black, white-tipped, as long as proboscis. Antennae light brown with pale yellow hairs.

Occiput black, covered with erect scales. In front, the scales are white, some of them narrow, curved, long, with ovate tip ; others are straight, truncated at tip, shorter and wider than the preceding ones. On the posterior half, which is more densely clothed, the scales are black or dark brown, truncated at tip. There are two long dark bristles at vertex of the head, where there is also a spot of silvery-white scale-like setae which project forward overhanging the basal antennal segments.

Prothoracic lobes dark ; a tuft of black erect scales with truncated tips at apex. Mesonotum : integument yellowish with grey pruinosity ; two small rounded black spots at the sides on the anterior half ; scales missing, except a few white, ovate, narrow, curved ones at the anterior border. Scutellum with black integument in the middle, whitish at the sides. Pleurae dark brown. Abdomen dark brown, nearly black, covered with pale golden hairs ; no scales.

Legs : front femora dark, spotted with yellow ; mid femora dark, white-spotted. Left femur missing ; the right one shows a characteristic tuft of black, erect, narrow, long scales around the distal third, not reaching the apex of the segment (fig. 1, *b*) ; many scales on basal two-thirds are missing but the remainder are black and lie flat. Inconspicuous white spot at the sides of femoro-tibial joint. Fore and mid tibiae yellowish, sprinkled with dark spots. Hind tibia dark on basal half ; distal half yellowish white. Front and mid tarsi (examined under low power lens) show a general straw colour ; under higher magnification one can distinguish the following details : first, second and third fore tarsal segments brown in the middle, white-ringed at both ends ; fourth and fifth, straw-coloured. Mid tarsi brown, with whitish narrow rings involving both ends of second, third, fourth, apex of first and base of fifth segments. On hind legs, the last three tarsal segments are missing ; first and second are dark brown.

Wings (fig. 1*a*) : Length 2·7 mm. The scales are narrow ovate. The general colour of the wing is white and light yellow, spotted with black. The light yellow scales are found on the anterior third and the white scales on the posterior two-thirds of the wing. The black spots are distributed as follows : along costa there are seven black spots, of which three small ones are located near the base of wing ; of these, the middle one is at the level of the humeral cross-vein ; three larger spots occupying costa, subcosta and first vein ; of these, the larger one, located near the tip of wing occupies also the anterior branch of second vein ; a small spot at tip of wing, at the level of anterior branch of second vein. The posterior branch of this vein has two indistinct dark spots near the ends. Third vein with two dark spots at the extremities. Fourth and fifth veins with inconspicuous black spots at all branches. Anal vein with two small black spots near the ends.

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* The studies and observations on which this paper is based were conducted with the support and under the auspices of the International Health Division of The Rockefeller Foundation and the Yellow Fever Services of Brazil and Colombia.

Holotype : One female, deposited in the entomological collection of the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil, under No. 2298.

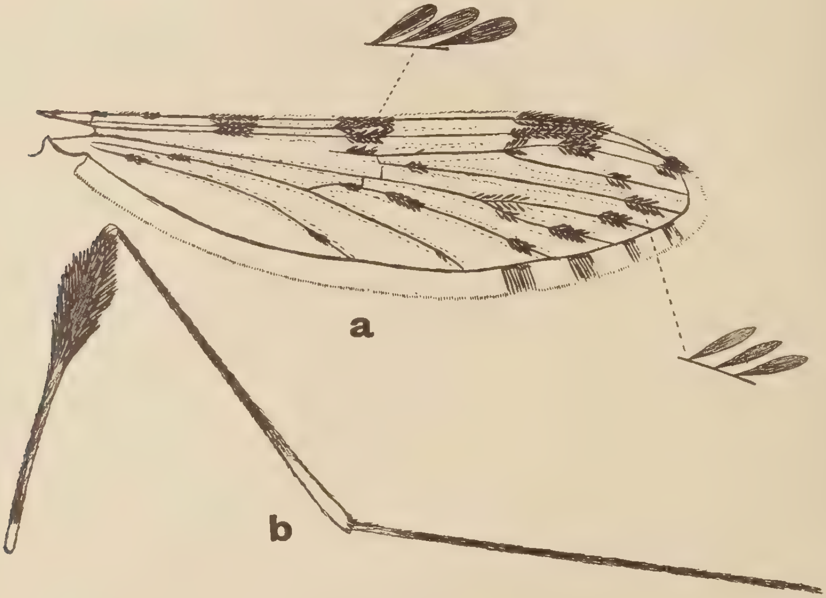

Fig. 1. *Anopheles squamifemur*, sp. n. : **a,** wing of female showing the dark spots ; **b,** hind leg of female showing the scale-tuft on hind femur.

Type locality : The only specimen we have, on which the foregoing description is based, was captured at the border of the forest with animal bait, in the early evening (6.30 to 7.30 p.m.), " vereda " Vegagrande, Intendencia del Meta, Municipio de Restrepo, Colombia, South America, 29th March 1935.

Taxonomic discussion.—Three species of *Anopheles* with scale tufts on the hind femora have been described up to now : *A.* (*Lophoscelomyia*) *asiaticus*, Leicester, in Theob., 1904 (Malaya), *A.* (*L.*) *annandalei*, Baini Prashad, 1918 (India) [var. *djajasanensis*, Brug, 1926 (Java) and var. *interruptus*, Puri, 1929 (Assam, Ceylon)] and *A.* (*A.*) *wellingtonianus*, Alcock, 1912 (Malaya).

A. squamifemur is easily separated from these species. The chief points are : (1) the wing markings are completely different ; while in *squamifemur* the wings are mainly white, black-spotted, in the other species they are mainly black with few white spots (4, Tafel VIII ; 3, Plate XXVIII ; 1, fig. 2) ; (2) the scale-tuft on the hind femora. In *annandalei* (and varieties) and *asiaticus* the hind femur has a large white scale-tuft at the tip, preceded by an area of outstanding black scales (4, Tafel VIII ; 3, Plate XXVIII). In *wellingtonianus* the " femora of the hind legs are distinguished by the presence of a very broad smooth band of small and closely adherent white scales, which runs into a prominent subterminal brush, or ruff, of long black scales " (Alcock 1912, p. 1 and fig. 1). As we have seen, the ornamentation of hind femora in *squamifemur* is quite different ; in this species there is a tuft of long black scales but no proximal band of tightly adherent white scales, nor distal white scale-like tuft.

As to the position of the present new species, the description of all its morphological characters shows that it may not be placed in any of the existing subgenera ; for this reason we were led to create a new subgenus which we have called *Lophopodomyia* from the chief character of the type species. Dr. Costa Lima, who examined the specimen, believes that a new genus might be created for the species, but as we only have a female specimen, he thinks it would be more convenient for the present to place the species in a new subgenus, which could be later confirmed or changed to a genus when the male genitalia are known.

Goeldia lanei, sp. n. ♂♀.

Male.—Proboscis moderate, about three-fourths the length of the abdomen, rather stout, brownish black with metallic green reflections in certain lights. Palpi very slender, long, a little shorter than the proboscis, dark brown with metallic green reflection. Clypeus broad oval, light brown, nude. Occiput covered with flat dark scales, showing silvery blue and green to yellowish green metallic reflections with the variation of the incidence of light ; a row of black, erect, forked scales behind ; black setae along the margin of the eyes ; two long bristles at vertex. Eyes black, contiguous at vertex.

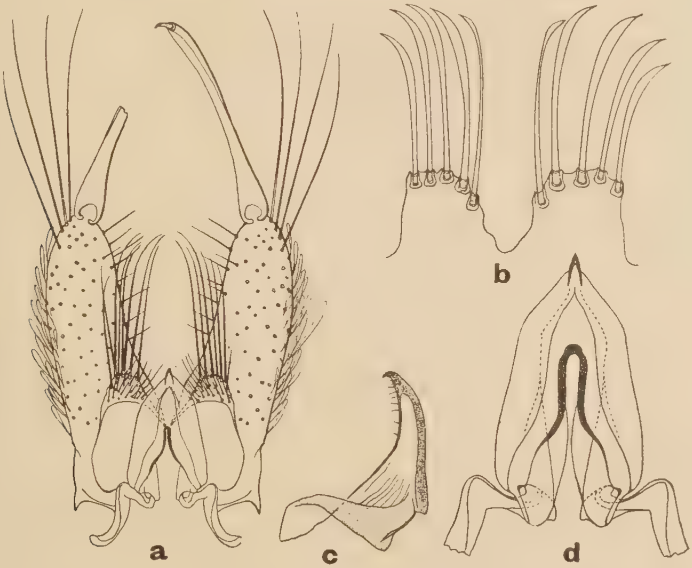

Fig. 2. *Goeldia lanei,* sp. n. : **a,** male genitalia, ventral view, except ninth tergite and tenth sternite ; **b,** *idem,* ninth tergite (more enlarged) ; **c,** tenth sternite ; **d,** mesosome (more enlarged).

Prothoracic lobes well separated, clothed with flat dark scales with silvery reflection. Mesonotum : integument brown ; vestiture of small brown-greenish, narrow curved scales. Dark brown bristles along the margins, chiefly near the root of wings, also present on prescutellar region. Scutellum clothed with flat, metallic blue-green scales. Postnotum brown, with a tuft of dark bristles behind. Pleurae and coxae with patches of broad, silvery-white scales ; on posterior pronotum the scales are ovate and golden yellow. Abdomen dorsally dark brown with metallic blue-green reflections ; venter yellowish white ; the dorsal and ventral colours are separated on the sides in an indented line, the white incising the dark posteriorly on the segments.

Wing scales ovate, small, moderately narrow, dark brown ; those at base of wing show metallic blue-green reflections.

Legs long, black with violet and blue reflections. Femora dark, light brown on inner surface. Hind tibiae with a white spot at basal extremity. Front tarsi dark. Mid tarsi with the second, third and fourth segments white on outer side, the inner side being dull yellowish on third and fourth segments and brownish on second ; fifth segment dark. Hind tarsi with a little more than the apical third of third segment and all of fourth and fifth pure white all round ; first segment with a white spot on outer side at basal extremity.

Genitalia : Side-piece cylindro-conical, with many long, stiff hairs. Basal lobes rounded, covered with short delicate hairs and many coarse, long stiff hairs along the upper margin, nearly reaching the apex of side-piece. Clasper slender, a little widened at base, long, with short, stout terminal spine. Tenth sternite longer than wide, thickened in one margin, the apex with only one pointed tooth ; short, delicate setae on membranous portion. Mesosome ovate, pointed at apex. Ninth tergites quadrate, well separated, bearing four or five moderately long, leaf-like setae.

Female.—Coloration as in the male. Palpi short, a little less than one-fourth the length of proboscis, dark brown with metallic green reflections.

The description is based on four males and one female ; the male specimens were bred from pupae collected from a bamboo joint, in the forest, Caney, 7th February 1935 ; the female was captured with horse bait, at 11 a.m., in the forest, Vegagrande, 23rd March 1935. Both localities belong to the Municipio de Restrepo, Intendencia del Meta, Colombia, South America.

Male *holotype* and female *allotype* deposited in the entomological collections of the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil, under numbers 2299 and 2300. Male *paratypes* to be deposited in the U.S. National Museum, Washington, D.C., in the Instituto de Hygiene, São Paulo, Brazil, and in the Laboratory of the Yellow Fever Service at Rio de Janeiro, Brazil.

Taxonomic discussion.—Based on the tarsal markings, we consider *Goeldia lanei* related to *longipes*, Fabr., *trichopus*, Dyar, and *leucopus*, D. & K., for it has the mid and hind tarsi white-marked. From them, however, it can be easily separated, not only by the morphology of the male genitalia, but also by the external characters of the adults, male and female.

Following Dyar's (1928) or Bonne & Bonne-Wepster's (1925) tables for adults, this species differs from *longipes* and *trichopus* by the absence of raised scales on hind tarsal joints. From *leucopus* it differs as follows : while this species has the apical third of fourth and all of fifth hind tarsal joints white, *lanei* has more than the apical third of third and all of fourth and fifth hind tarsals pure white.

As to the male genitalia, following Dyar's key (1928), the difference appears in the first item ; the basal lobe of side-piece is short-haired in the above-mentioned species, while in *lanei* this lobe bears long hairs. Besides other details, which can be verified by the comparison of the descriptions and figures, it must be emphasized that the number of teeth at the apex of the tenth sternite is different ; *lanei* has only one tooth, while in the other three species there are four or five teeth.

This species has been named after my close friend John Lane, of the Instituto de Hygiene de São Paulo, Brazil.

Acknowledgments.

I am very grateful to Dr. Costa Lima for his invaluable help in the study of *Anopheles squamifemur*. I am also indebted to Mr. N. Cerqueira of the Laboratory of the Yellow Fever Service at Rio de Janeiro, who furnished the drawings that illustrate this paper.

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CLIMATE, THE VITAL FACTOR IN THE ECOLOGY OF *GLOSSINA*.

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(Plates III–V.)

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From 1927 to 1932 the writer carried out research on the ecology of *Glossina morsitans* at Kikori, in Tanganyika Territory, obtaining most of his results from perennial censuses of the tsetse population (fly-rounds), and from other lengthy experiments upon breeding, concentration, etc. A special technique was devised, and the collection of meteorological data played an important part in the work, which has already been described (Nash 1930, 1933a).

From 1933 to 1936 the writer has been working at Gadau, in Northern Nigeria, and has made a similar investigation into the ecology of *G. submorsitans* and *G. tachinoides*, which forms the subject of Part I of the present paper. Part II deals with a summarised ecological comparison of the eastern and western races of *G. morsitans**; the writer puts forward tentative suggestions as to the climatic limits of the species, and indicates the existence of fundamental laws which control the species throughout its African range.

PART I.

THE ECOLOGY OF *G. SUBMORSITANS* AND *G. TACHINOIDES* IN WEST AFRICA.

INTRODUCTION.

1. Definitions of the Terms employed.

Some of the following terms have already been defined (Nash 1933a), but have now been slightly modified so as to make them suitable for both East and West African conditions ; others have been coined in an endeavour to avoid introducing native names into scientific literature.

" True Habitat " (Primary Focus). The true habitat is the main breeding area and home of the tsetse ; it should offer considerable protection to the fly against fires, floods, and high temperature. Islands of residual forest form the true habitat locally, but elsewhere in Nigeria it is frequently represented by thick riverine vegetation on the banks of streams which contain permanent water or pools.

" Residual Forest " (Fringing Forest, Kurumi). The residual forests are the only surviving remnants of the original forests of the country, and are represented by small islands of partly evergreen trees with crowns united by lianes to form a high shade canopy ; these islands are bounded and cemented together by peripheral and intrusive thickets of thorny creepers, and are rarely very far from water. Residual forest forms the perfect true habitat—impenetrable to fire, elevated above flood-level and providing protection against the sun and desiccating winds (Plate V, fig. 1 ; Plate IV. fig. 4).

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* Major E. E. Austen considers that individuals from East and West Africa are merely different forms or races of the same species, but the writer retains the name *submorsitans* for the West African race in Part I, as it facilitates description.

" Temporary Habitat." This is a temporary breeding area and home for tsetse during the rains and early dry season ; it is evacuated during the hot weather. Thickets bordering temporary ponds (secondary foci), or heavy woodland savannah containing small thickets, form the temporary habitats locally, although elsewhere in Nigeria they are frequently represented by riverine vegetation clothing stream banks in reaches where the stream will later become dry.

" Meadow-pan " (Vlei, Mbuga, Fadama and Fako). A formation that in the rains is luxuriant swampy meadow, and in the dry season is an open expanse of pan with hard, cracking, black-cotton clay, from which the grass has usually been entirely destroyed by fire (Plate IV, figs. 1, 2).

" Woodland Savannah." A term used somewhat vaguely to describe the general, low, mixed woodland that covers the sand-ridges which form the bulk of this part of Nigeria. As regards shade and visibility it is comparable to the *Berlinia-Brachystegia* woodland of East Africa, but it supports a much more luxuriant grass-growth in the rains and consequently burns more readily (Plate V, fig. 2).

" Fly-round." A fly-round, of the type used by the writer, is a survey of tsetse-fly over a fixed route, repeated at definite short intervals throughout the year.

2. Tsetse Distribution in Northern Nigeria.

This paper would not be intelligible to any one accustomed to East African conditions until certain points had been emphasised.

In northern Nigeria there are great areas of woodland savannah and even of *Isoberlinia doka* which closely resemble the enormous *Isoberlinia-Brachystegia* fly-belts of East Africa ; yet, owing to the extreme climatic conditions prevailing in the West African hinterland, these areas of similar woodland are fly-free except in the immediate vicinity of stream-beds fringed with riverine vegetation. Even the wet season spread of *G. submorsitans* is incapable of penetrating the woodland for more than a few miles from the riverine true habitats ; the reason is that this species has not time to colonise extensively, because the rains are of very short duration, and are closely followed by hot weather which destroys the bulk of the population and drives the survivors back to the true habitat. In this country fly-belts are always linear, because they follow the water-courses ; the country between rivers is fly-free.

The Gadau fly-belt is entirely dependent on the Katagum River, which supports islands of residual forest in the flat river-plain. These diminutive patches of forest are the key to the local fly problem, and their importance cannot be over-emphasised ; if there was no residual forest there would be no fly in the area. The shallowness of the river-bed and consequent annual flooding of the meadow-pan has resulted in a belt on each bank several miles in width, which can support tsetse owing to the presence of these patches of residual forest growing around pools and the fringes of drainage depressions. This is not typical of northern Nigeria, but rather of the Katagum River, which is characterised by a slow current and shallow bed as it nears Lake Chad ; elsewhere the country is usually not so flat, with the result that streams with steep banks choked with riverine vegetation are numerous and support *G. tachinoides*—or *G. palpalis* further south ; tsetse are confined to the immediate vicinity of these streams.

The meadow-pan in northern Nigeria does not assume the same importance in tsetse bionomics as in East Africa, where it frequently acts as a feeding-ground and concentration centre ; this is again due to the extreme climatic conditions of the West Coast hinterland, which closes the open meadow-pan to tsetse for many months of the year.

3. Situation and Soils of the Gadau Area.

Gadau (12°N., 10°E.) is situated 115 miles east of Kano in Northern Nigeria. About 120 miles S.W. of Gadau is the northern escarpment of the high Bauchi plateau (3,500 ft.), which intercepts the S.W. monsoon, causing it to lose much of its rain before it reaches this district. Gadau lies in the Lake Chad basin amid country that is almost flat and only 1,200 feet above sea-level ; it is situated in the transition between the Woodland Savannah belt and the Thorn Forest and Desert belt. Undulating sand ridges, supporting a fairly dense low woodland, are typical of the area ; meadow-pan of " black-cotton " clay is common in depressions between these ridges, and is of considerable extent near the large, sandy Katagum River, which only flows for some five months in the year. This is the only river in the neighbourhood and, owing to the flatness of the country, no tributary streams run into it with the exception of the meadow-pans and drainage depressions which conduct slow-moving sheets of water into the main river ; for ten months in the year these drainage depressions are dry, except for rare pools.

In the past the whole of this country was part of Lake Chad, which accounts for the deposits of alluvium ; the complete absence of any surface rock or even small stones is very striking.

4. The Seasons.

There is one long dry season and one wet season.

The Dry Season (October to April).

A very pronounced season. During seven years the five months, November to March, have been rainless ; the season starts with two months of hot humid weather, then three months of dry cold, and finishes with two months of very hot desiccated conditions, viz. :—

1. Early Dry Season (October and November). The country rapidly dries up and temperatures up to 102°F. may be recorded. During November the nights become much colder, and big diurnal temperature ranges occur. Grass fires start at the end of this season.
2. Cold Season (December to February). Very low temperatures occur near dawn, 40°F. being the lowest recorded. The days vary from bright and warm to being completely overcast with a fine dust which is carried by the dry harmattan wind ; sometimes the sun is obscured for a week at a time, and the temperature may not rise all day above 74°F. (Plate IV, figs. 5, 6). The weather gets much warmer in February and the transition from cold to hot is very rapid.
3. Late Dry Season (March and April). In March enormous diurnal variations in temperature occur ; a range of 50·5°F. (from 58·5° to 109°F.) has been recorded between 6 a.m. and 3 p.m. of the same day. The atmosphere is also very dry at this season ; using a whirling psychrometer I have recorded on the forest's fringe a 7 per cent. relative humidity at 102°F., and once a saturation deficiency of 71·24 millibars at 107°F. Buxton & Lewis (1934) record that for April 1933 the mean relative humidity at 2 p.m. was under 20 per cent. With the advent of the first tornado in April the humidity rises, but the temperature remains very high.

The Wet Season (May to September).

The average Gadau rainfall is nearly 33 inches, 20 of which fall in July and August (see Table I) ; the average number of wet days is only 57. The wet season may be divided into the early and heavy rains.

1. The Early Rains (May and June). The late dry season merges into the early rains, which consist of a sequence of periods, each characterised by the weather becoming progressively hotter and more sultry until a tornado brings temporary relief ; as the season advances the frequency of these storms increases, resulting in cooler conditions towards the end.

2. The Heavy Rains (July and August). A season characterised by cool days, warm nights, torrential storms and extensive flooding of the meadow-pan formation (Plate IV, fig. 3).

TABLE I.

Average Monthly Rainfall over 6 *Years at Gadau Laboratory* (1930–1935).

Months	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	Ann. av.
Average rainfall (inches) ...	0·0	0·0	0·0	0·5	2·8	3·9	8·7	11·9	4·1	0·9	0·0	0·0	32·8

5. Description of the Investigation.

In May 1933, an area of bush was found which had never been disturbed by the earlier research workers, and which was little frequented by natives. A fly-round, 3¾ miles in length, was immediately marked out and divided into seven sections according to the vegetation types which were tapped by the path. (For fly-round technique see Nash 1930.)

The first section of the fly-round follows the foot of a sand ridge which borders the river-plain—at this point nearly 3 miles in width ; from sections 2 to 5 the route crosses the plain and consists of two sections of meadow-pan and two of heavy woodland savannah ; it then reaches the residual forest or true habitat, which is only half a mile from the Katagum River. Section 6 taps the fringe of the forest, whereas section 7 follows a path cut through the centre of the forest. Throughout this paper sections 1 to 5 are grouped together as the " open woodland sections," and sections 6 to 7 as the " forest sections."

The residual forest, which lies half a mile south of the Katagum River, consists of a series of adjacent forest islands situated along the edge of a drainage depression which holds water for about five months in the year. Only two of these patches of forest are of any size : Dogon Kurumi is the largest, being 550 yards long by 30 to 150 yards wide, and is thoroughly tapped by the fly-round ; Kuramin Gundun is 640 yards long but usually only a few yards in width, and is reserved as a control for a future clearing experiment, which does not come into the scope of this paper. Since there is no other residual forest capable of forming a true habitat for about five miles, this strip can be regarded as the dry season sanctuary of the local tsetse community, and hence as the key to the proper understanding of the local problem. It is estimated that at least half of the total forest is thoroughly tapped by sections 6 and 7.

Catches are made along the fly-round route from four to six times a month and yield data upon the seasonal fluctuations in the size of the population, the seasonal distribution of the population, the sex proportion, nutrition and game distribution, and some indirect evidence upon the breeding season.

Two meteorological stations were erected at the beginning of the investigation, one in the open meadow-pan in which tsetse only occur in the rains and early dry season, and another inside the residual forest or true habitat (Plate IV, figs. 1, 2 ; Plate III, fig. 1) ; hence the meteorological factors are recorded in the two extremes of the tsetse's distribution. Both stations are equipped with Stevenson screens, containing recording thermo-hygrographs checked by accurate dry and wet bulb hygrometers, and with Livingston white atmometer spheres ; all instruments are kept at four feet above the ground-level. The recording thermo-hygrographs yield data upon maximum, minimum and mean temperature, as well as upon saturation deficiency, which is obtainable from the readings of the dry and wet coil pens ; the atmometers record the evaporating power of the air. In addition to these instruments, the meadow-pan station has a rain-gauge. Data collected upon the maximum temperature in microclimates within the forest have already been published (Nash 1936a).

The mean monthly temperature and saturation deficiency figures quoted in this paper have been derived from planimeter measurements of the areas enclosed by the curves recorded on the thermo-hygrograph charts ; similarly, the evaporation figures represent a continuous record throughout day and night.

The data given by the fly-rounds has been supplemented by puparia rounds, marked fly experiments, and other methods devised to fill in the gaps left in this study of the ecology of *G. submorsitans* and *G. tachinoides*.

The Seasonal Factor.

1. A Comparison of the Climate in Forest and Meadow-Pan.

Owing to the tsetse's enforced evacuation of the open country and its concentration in the true habitat during the late dry season, a comparison of the meteorological

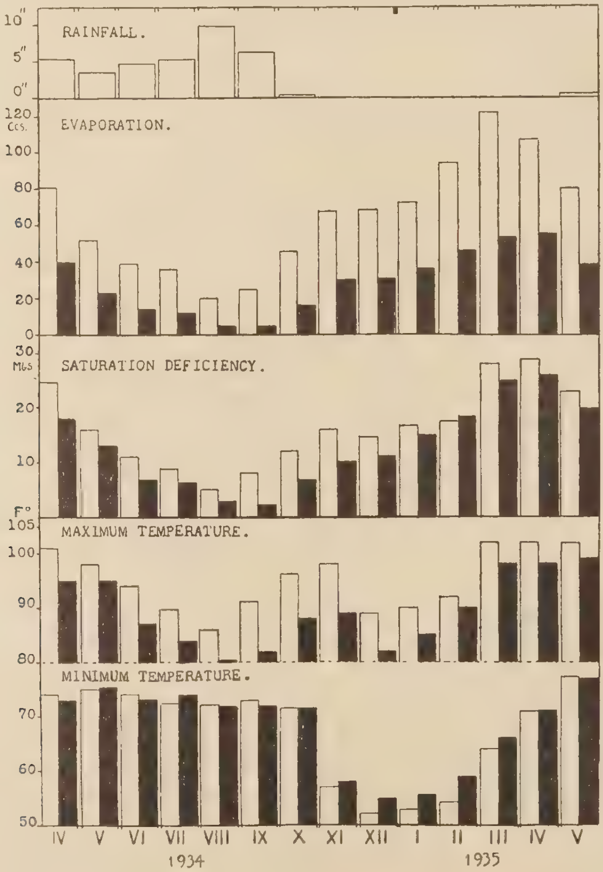

Fig. 1. A comparison of the climate in meadow-pan (white) and in residual forest (black).

records from the Meadow-pan and Residual Forest Stations shows what climatic conditions are supportable and what insupportable to the fly community. In March, April and May the tsetse cannot exist in the open country, but they can exist in the forest.

The mean monthly meteorological figures for each station are shown side by side in fig. 1. A period of 14 months has been specially selected so as to show the effect upon the other factors of the rains breaking early, as in April 1934, or late, as in 1935 ; if the rains are late the severe conditions at the end of the dry season are prolonged and accentuated (*cf.* April and May 1934 and 1935). Rainfall has been measured only in the Meadow-Pan Station, but the other factors will now be dealt with separately.

Evaporation.—The meadow-pan atmometer is exposed to full sunlight, but the forest instrument receives only the filtered sunlight that penetrates the high shade canopy ; this difference in exposure to the sun probably accounts for much of the disparity in the readings from the two stations.

When the rains started in April 1934, the evaporation in the meadow-pan was only twice that of the forest, but as the rainfall increased, so the difference became steadily more marked, being four times greater by August. This is understandable, because the shade canopy of the forest increases with the rains, reducing the amount of sun that reaches the atmometer sphere, whereas the Meadow-Pan Station being in the open is not affected by increased foliage. In September, when the rains are ending and hot days with brilliant sun are common, the open country starts to dry up with great rapidity, whereas the sheltered forest remains wet and sodden, and consequently in this month the difference is greatest, the evaporation in the meadow-pan being five times that of the forest. As the dry season advances and the forest floor loses its moisture, so the difference between the inside and outside of the forest decreases, until by January the evaporation in the meadow-pan is only twice that of the forest ; approximately this ratio is maintained until the next rains. Despite the lack of rain in April 1935 the evaporation decreased in the meadow-pan but not in the forest ; this was probably due to the cessation of the harmattan wind which would not affect the sheltered forest.

Saturation Deficiency.—The difference in the readings from the two stations is not nearly so striking ; but these readings are obtained under similar shade conditions, the thermo-hygrographs being housed in Stevenson screens in each station.

In April 1934, the difference between the Meadow-Pan and Forest Stations was abnormally great ; the rain from the three heavy thunderstorms of this month dried up almost immediately in the open country, but was retained by the shaded forest floor, resulting in increased humidity for a considerable time ; later, when the wet days become more frequent, the open country also retained its moisture and the difference became less marked.

The period of greatest difference is at the end of the rains and early dry season, September to November inclusive ; the meadow-pan rapidly dries up and the humidity rapidly falls, but the sheltered forest retains its moisture and high humidity for some months. Once the forest floor has dried up the difference in saturation deficiency readings varies but little in the two stations.

Maximum Temperature.—Fig. 1 shows that the dry season is mainly a season of high maximum temperatures, interrupted, however, from December to February by a period of relatively cold weather.

Here again the difference in the two stations is most pronounced at the end of the rains and early dry season, when the evaporation from the wet forest floor keeps the temperature down in the forest, and prevents it heating up as quickly as in the open country. The coldest part of the cold season (December and January) is also a time of great differences in the maximum temperatures. It is suggested that at this season of very cold nights, when haze usually hides the sun until nearly mid-day, the forest has not sufficient time to heat up before the sun sets, whereas the temperature in the open, shadeless country reacts at once to one or two hours of sunshine.

Minimum Temperature.—Fig. 1. shows that the minimum temperature remains steady from the break of the rains until the approach of the cold season. Readings from the two stations show no consistent differences except from November to March when the nights are cold ; at this season the forest is always rather warmer.

General Comparison.—It will have been noticed that the difference between the readings from the two stations is least in the late dry season, when the climate is most severe ; hence at that season, when tsetse cannot live in the open country, they must be surviving in the forest by only a very narrow margin. This has already been shown in the case of maximum temperature (Nash 1936a). The real value of the forest to the fly community is, however, that the period of stress due to extreme climatic conditions is far shorter in the forest than in the meadow-pan ; for example, taking the mean monthly readings for the year June 1934 to May 1935 :—

1. The evaporation was over 50 cc.f or 7 months in the meadow-pan, as compared with 2 months in the forest.
2. The saturation deficiency was over 10 millibars for 9 months in the meadow-pan, as compared with 6 months in the forest.
3. The mean maximum temperature was over 90°F. for 8 months in the meadow-pan, as compared with 3 months in the forest.
4. The mean minimum temperature was under 55°F. for 3 months in the meadow-pan, but never under 55°F. in the forest.
5. The mean monthly temperature was over 80°F. for 6 months in the meadow-pan, as compared with 3 months in the forest.

The residual forest is never so hot, so cold, or so desiccated as the meadow-pan. At the only time of year when possibly the forest is too humid for tsetse it can be evacuated in favour of the open country.

Northern Nigeria must be approaching the climatic limit for the range of *G. submorsitans* and *G. tachinoides* ; for this reason all the summaried meteorological data collected are given by months in Tables II to VI, since it should be of interest to students of tsetse distribution.

TABLE VII.

To show the extreme Weekly Means recorded during the Investigation.

Meteorological factors recorded	Highest week recorded		Lowest week recorded	
	Meadow-pan	Forest	Meadow-pan	Forest
Maximum temperature	107·0°F.	103·4°F.	76·3°F.	72·4°F.
Minimum temperature	79·8°F.	79·3°F.	47·2°F.	50·4°F.
Mean temperature	89·5°F.	88·0°F.	64·0°F.	63·0°F.
Saturation deficiency	33·33 mb.	32·06 mb.	2·91 mb.	0·91 mb.
Evaporation	129 cc.	59 cc.	9 cc.	2 cc.

The highest and lowest weekly records ever experienced during this investigation are given in Table VII, as they give a better idea of the extreme conditions which the tsetse may have to face for a short period.

TABLE II.

Average Mean Monthly Maximum Temperature (1934 *and* 1935).

Months	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	Period	Annual average
Meadow-pan	87·8	91·1	101·6	101·5	100·0	94·0	89·6	86·1	90·5	97·0	97·2	90·1	2 years	93·9°F.
Forest	82·2	86·7	97·3	96·8	97·0	88·9	84·0	79·5	81·2	87·2	88·0	83·0	2 years	87·7°F.

TABLE III.

Average Mean Monthly Minimum Temperature (1934 *and* 1935).

Months	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	Period	Annual average
Meadow-pan	52·8	53·6	63·8	72·7	76·3	74·8	72·9	72·6	73·8	69·9	57·6	53·0	2 years	66·1°F.
Forest	54·8	56·7	66·3	72·2	76·3	74·0	73·7	71·5	72·4	70·5	58·5	55·5	2 years	66·9°F.

TABLE IV.

Average Mean Monthly Temperature (1934 *and* 1935).

Months	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	Period	Annual average
Meadow-pan	69·6	71·8	82·2	86·5	86·4	83·0	79·9	77·7	80·5	81·5	76·0	70·1	2 years	78·8°F.
Forest	68·3	71·7	81·1	83·8	85·1	80·2	77·6	74·9	76·2	77·7	72·2	68·5	2 years	76·4°F.

TABLE V.

Average Mean Monthly Saturation Deficiency in Millibars (1934 *and* 1935).

Months	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	Period	Annual average
Meadow-pan	15·36	19·07	27·69	26·89	19·44	12·95	9·69	5·71	7·88	12·76	16·54	14·74	2 years	15·73
Forest	13·23	18·40	24·79	22·13	16·45	9·33	6·07	2·74	2·39	7·21	11·22	11·45	2 years	12·12

TABLE VI.

Average Mean Monthly Evaporation in cc., using a Livingston white spherical Atmometer (1933 *to* 1936).

Months	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	Period	Annual average
Meadow-pan	68	87	107	91	64	42	29	17	23	48	66	66	3 years	59
Forest	32	41	50	46	29	18	10	4	5	17	26	29	3 years	26

2. Concentration as related to Season.

Seasonal Distribution of both Species.

In fig. 2 the shaded area represents the residual forest, and the black columns the mean monthly evaporation within the forest. The unshaded area above represents the open woodland, and its evaporation is similarly shown. The solid-lined curve gives the percentage of the total monthly catches of *G. submorsitans* which came from the five open woodland sections ; the dotted curve shows the same for *G. tachinoides*.

Percentages have been deliberately used, as by bringing the data into the form of a proportion fluctuations in the size of the population are ignored. A series of increases in the monthly percentage of the catch that occurs in the open country can be regarded as proof of the fly spreading outwards from the residual forest, whereas a decreasing percentage denotes concentration ; hence the curves show the seasonal ebb and flow for three years.

Annually the two species spread out during the early rains and attain maximum dispersal in August and September, when evaporation is lowest ; then the rains end, evaporation in the open country soars up, and the range of the species gradually becomes restricted to the vicinity of the forest sanctuary. The evacuation of the open country continues throughout the dry season, becoming almost complete in March and April, when both temperature and evaporation are highest.

It will be seen from fig. 2 that even in August and September 1934, when 90 per cent. of the *G. submorsitans* were out in the open country, only 20 per cent. of the *G. tachinoides* were out ; whereas in March and April 1935, when only 8 per cent. of the *G. submorsitans* remained out, not a single *G. tachinoides* could be found outside the forest. The fact that *G. tachinoides* is essentially a forest species is emphasised by the figures taken over 3½ miles of fly-round during two years—out of 17,000 *G. tachinoides* caught, only 7 per cent. came from the open woodland sections ; out of 30,618 *G. submorsitans* caught, 46 per cent. came from the open woodland sections.

The wet season spread was greatest in 1934, when the *G. submorsitans* curve was over the 50 per cent. line for 9 months, as compared with only one month in the rains of 1935. Table VIII indicates that the degree of spread is not related to the total rainfall, but to the number of wet months ; this is only to be expected, because the rains are the favourable season for tsetse (see later), and the longer the wet season lasts the further the fly are able to disperse.

TABLE VIII.

Year	Total rainfall	No. of wet months (over 0·2 in.)	No. of months when over 50 per cent. of catch in open woodland
1933	42 inches	6 months	2 months
1934	35 ,,	7 ,,	9 ,,
1935	25 ,,	5 ,,	1 month

There is always a considerable lag between the start of the rains and the beginning of fly dispersal ; hence when the rainfall is concentrated over a very short period, as in 1935, the tsetse have no sooner started to extend their range than the rains end and they are forced back again to the forest.

Fig. 2 suggests the existence of a close relationship between evaporation and fly dispersal and concentration ; further, there would appear to be a lag, since maximum dispersal usually occurs a month after minimum evaporation, and, conversely, minimum dispersal (maximum concentration) occurs a month after maximum evaporation.

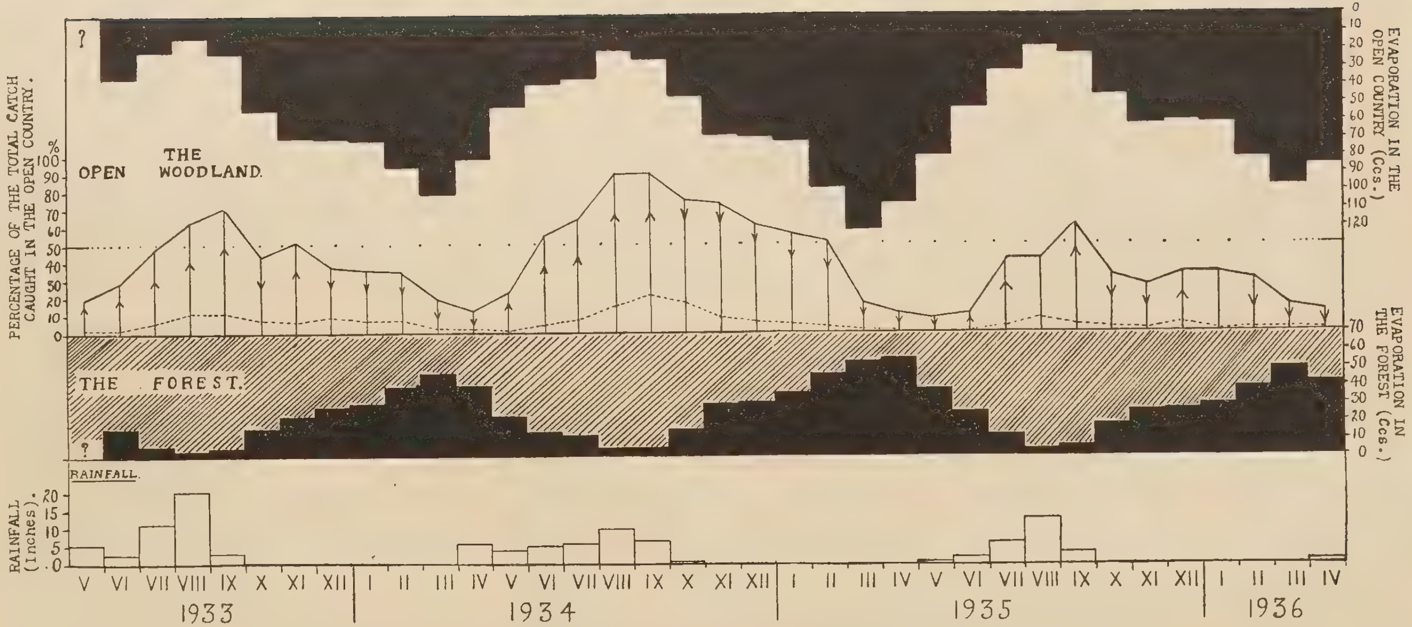

Fig. 2. The seasonal expansion and contraction of communities of *G. submorsitans* (solid curve) and *G. tachinoides* (dotted curve).

TABLE IX.

Relationship between Seasonal Dispersal and Climatic Factors (G. submorsitans *and* G. tachinoides).

Percentage of catch in open country	Mean evaporation cc.			Mean saturation deficiency Millibars			Mean maximum temp. °F.			Mean minimum temp. °F.			
	No. of months	Same	Previous	No. of months	Same	Previous	No. of months	Same	Previous	No. of months	Same	Previous	
Up to 20	8	91	95	8	24·5	24·0	8	101	99	8	70	63	*G. submorsitans.*
21–40	9	65	60	8	16·4	15·6	9	93	93	9	58	61	
41–60	8	50	48	5	12·6	14·7	5	90	92	5	66	66	
61–80	7	39	33	5	12·0	10·8	5	93	93	5	66	70	
81–100	2	23	28	2	6·5	6·9	2	89	88	2	73	72	
Up to 5	20	68	70	19	18·7	18·5	19	96	95	19	66	64	*G. tachinoides.*
6–10	10	56	50	6	13·6	13·9	8	79	82	8	52	55	
11–15	3	18	23	1	5·0	8·8	1	86	90	1	72	73	
16–20	1	46	25	1	12·1	7·9	1	97	91	1	71	73	
21–25	1	25	20	1	7·9	5·0	1	91	86	1	73	72	

The relationship is investigated in greater detail in Table IX, which was suggested to the writer by Professor Buxton. Referring first to the upper half of this table, which deals with *G. submorsitans*, the percentage of the total fly-round catch which was taken in the open woodland sections has been arranged in five groups, ranging from 0–100 per cent. The average of the monthly meteorological figures, for all the months in which the percentage figures fell in a certain group, has been placed against that group in the table ; for example, there were 8 months in which the percentage of the catch taken from the open country lay between 0 per cent. and 20 per cent. and the average evaporation for the corresponding months was 91 cc., whilst the average evaporation of each of the months immediately previous to the months in which the catches were made was 95 cc. Similar data for saturation deficiency and both maximum and minimum temperature are also shown. If a good relationship exists between fly dispersal and a meteorological factor, then there should be a consistent rise or fall in the climatic mean corresponding directly or inversely with the rise in the percentage.

The results for *G. submorsitans* are interpreted as follows :—

Evaporation.—An excellent inverse relationship exists between increasing dispersal and the decreasing evaporation of both the same and previous months. Dispersal is maximal, when evaporation is minimal, and minimal when evaporation is maximal. Note that dispersal is maximal when the evaporation in the open country is near the optimum zone of 20–25 cc. (Nash 1933a).

Saturation Deficiency.—Another excellent inverse relationship ; the data for the months previous to the catches give a better gradation.

Maximum and Minimum Temperature.—Neither factor gives a close relationship. Admittedly a certain affinity exists between dispersal and temperature, but the imperfections in the relationship suggest that temperature is only indirectly effective in so far as it plays an important part in determining the degree of saturation deficiency and evaporation.

The lower half of Table IX gives similar results for *G. tachinoides*, but the limited dispersal of this species causes the bulk of the data to fall into the first two groups (0–10 per cent.), leaving most inadequate data for the remainder of the table ; however, it can be said that a fair relationship exists between fly dispersal and evaporation of the previous months, and that an excellent affinity exists with saturation deficiency of the previous months. Neither maximum nor minimum temperatures appear to bear any relationship to dispersal. In so far as they go, the results for *G. tachinoides* agree with those for *G. submorsitans*.

At Professor Buxton's suggestion a copy of the original data from which Table IX was constructed will be deposited in the library of the London School of Hygiene and Tropical Medicine.

Conclusions.

1. *G. submorsitans* tends to evacuate the forest and to spread out into the open during the rains ; dispersal is greatest at the end of the rains.
2. As the dry season advances the range of *G. submorsitans* becomes restricted to the vicinity of the residual forest ; concentration is greatest at the end of the dry season.
3. *G. tachinoides* is a forest and thicket fly, and its wet season dispersal into open country is very limited ; *G. submorsitans* is an open woodland fly which is temporarily forced into the forest when compelled by the climate.
4. The extent of the annual dispersal is indirectly governed by the duration of the wet season ; the longer the season, the greater the dispersal.
5. The dispersal of *G. submorsitans* and *G. tachinoides* is closely associated with the evaporation and saturation deficiency of the previous month, and, to a lesser extent, of the same month ; dispersal yields to concentration as the evaporative power of the air increases. Maximum and minimum temperatures only affect dispersal indirectly in so far as they influence evaporation and the saturation deficiency.

The Seasonal Movements of G. submorsitans *between the Residual Forest and the surrounding open Woodland.*

The data used in this section have been obtained from an entirely different source, having been acquired from a fly-marking experiment.

Four times a month tsetse were marked with oil paints in and around the residual forest and were then liberated. About 4 per cent. were eventually recaptured while the fly-rounds were being visited, and the sections in which they were recaptured were noted. The total fly marked in the month and the subsequent recaptures yielded data from which the percentage of recaptures taken in each section of the fly-round was obtained ; these figures have been placed against the month when the flies were marked.

In fig. 3 the fly-round sections are represented diagrammatically as concentric circles ; the innermost circle represents the residual forest (vii) ; the next circle represents the forest fringe (vi), and so on until the outer circle which represents the

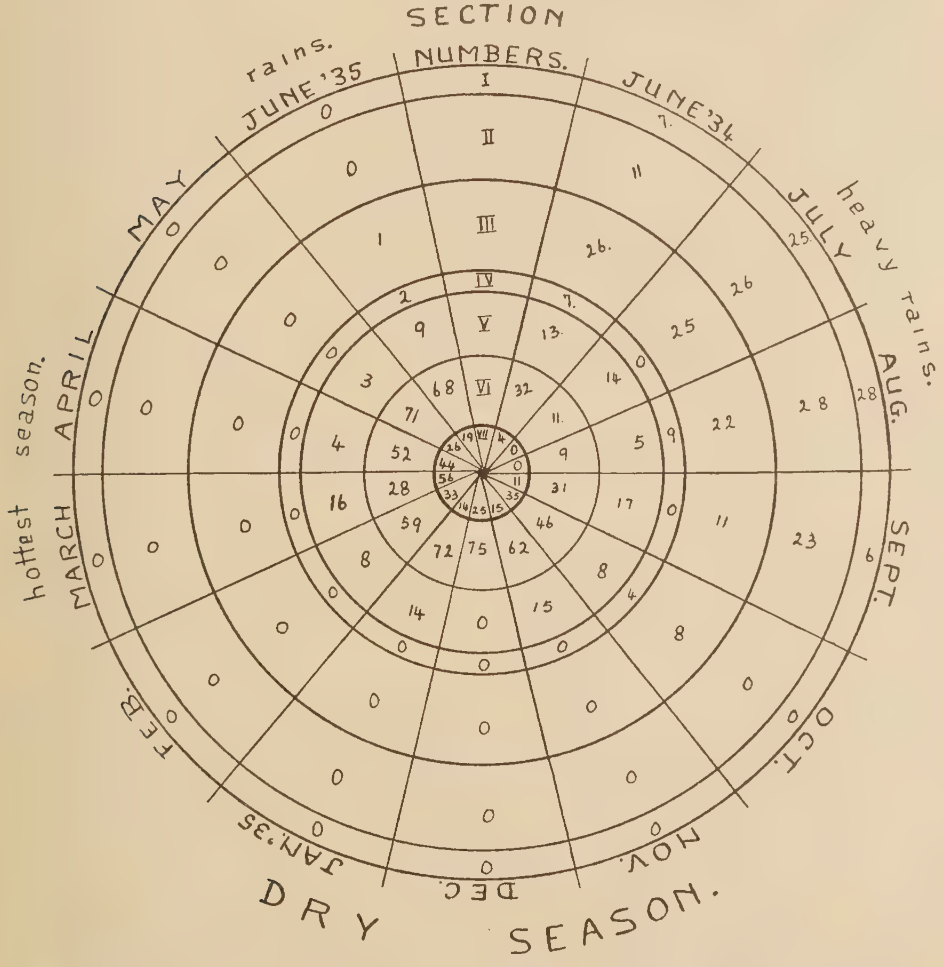

Fig. 3. The seasonal movements of *G. submorsitans* between the residual forest and the surrounding open woodland.

section furthest from the forest sanctuary. In the sector at 12 o'clock each concentric circle is labelled with the number of the fly-round section which it represents ; all the concentric circles are subdivided into thirteen further sectors, one for each of the thirteen months dealt with.

The diagram is to scale, in that the distance between the circles is proportional to the length of the fly-round sections which they represent. The numbers within each sector or month represent the percentage distribution of the month's total recaptures ; *e.g.*, starting from Sect. I and working inwards to Sect. VII, the percentage distribution of the June 1934 recaptures was 7, 11, 26, 7, 13, 32 and 4 per cent. The chief value of this diagram is that one can also follow the annual history of each individual section by reading clockwise from June 1934 to June 1935, thus :—

Section I.—The number of flies that have reached this section from the place of marking in the forest 2½ miles away steadily increases from 7 per cent. in June 1934 up to 28 per cent. in August, the wettest month ; the rains end in September, and for the next 9 months no more tsetse succeed in reaching this section.

Section II.—As for Sect. I, but being nearer the forest, colonists still reach it in large numbers in September.

Section III.—As for Sect. II, but being still nearer the forest, marked fly continue to reach it until October 1934. It is then inaccessible to flies from the forest until June 1935, when the first individuals of the next wet season arrive.

Section IV.—It is advisable to ignore this very small section of only 293 yards in length, as the numbers of recaptures were very small.

Section V.—This meadow-pan section surrounds the forest, and so is always accessible to the fly, even when they are concentrated in the forest and unable to spread any distance to the further sections.

Section VI represents the forest fringe or true habitat of *G. submorsitans*. In July and August, the wettest months, the forest fringe is almost deserted by fly marked both here and inside the forest ; presumably at this season fly, immediately after marking, tend to spread out and rove far away. From September to February (the early dry and cold season) the bulk of the marked fly congregate in this section, but in March, the hottest month, even the forest fringe is too hot, and a large proportion of the marked fly enter the forest (see Sect. VII). In May and June (1935) the flies start to go out again and the percentage increases on the forest fringe—Sect. VI.

Section VII—inside the forest. In the heavy rains, July and August, the sodden forest is evacuated, but flies re-enter the forest in the early dry season in small numbers. In the hottest months, when even the forest fringe is too hot, many marked fly concentrate inside the forest (see March 1935). In May and June they start to spread out as the rains break.

Conclusions.

1. During the heavy rains flies marked in the vicinity of the forest do not stay there but rove through the bush and reach the remotest sections of the fly-round in considerable numbers.
2. At the end of the rains the distance which can be reached by the marked fly rapidly decreases, until they become isolated in the vicinity of the forest, where they remain throughout the dry season.
3. In the hottest part of the late dry season, even the forest fringe becomes too inclement, resulting in large numbers of recaptures being made inside the forest.
4. As the new rains break in May and June the fly first concentrate on the forest fringe and then start to penetrate into the nearest woodland.

3. Fly Activity as related to Season.

Many tsetse workers have suggested that at certain times of day fly were less active than at others, but no serious work seems to have been done on the subject except by Morris (1934) when he was working on *G. longipalpis* in the Gold Coast ; he found that fly activity was correlated with temperature. In order to discover the true diurnal cycle of fly activity and whether the cycle varies according to the season, the following experiment was devised :—Two paths were made, 100 yards in length, one passing along the fringe of the residual forest and one passing through its centre. Between 6 a.m. and 6 p.m., hourly five-minute catches were made on each path, and at the same time dry and wet bulb readings were taken with a whirling psychrometer. Immediately after counting each catch the fly were liberated, so as to prevent any depletion of the population ; it is unlikely that depletion took place, as frequently the morning and evening catches were equally large. The experiment was carried out once or twice every month during a year.

Owing to lack of space it is impossible to show graphically the diurnal activity cycles for each month ; hence graphs have been selected which are considered typical of the cycles obtained during each of the five seasons. Unfortunately the numbers of *G. submorsitans* are too low to be of much value except when fly are concentrated near the forest in the late dry season and early rains.

In fig. 4 the size of the hourly catches has been plotted against the time of day when the catch was made ; a graph is given for both species of tsetse for every season. The solid curve labelled " in " gives the catch for the inside of the forest (the true habitat of *G. tachinoides*), and the dotted curve labelled " out " represents the catch from the outside edge of the forest (the true habitat of *G. submorsitans*).

Heavy Rains.—*G. tachinoides* are active at dawn, but activity rapidly increases as the temperature rises, becoming maximal between 12 and 2 p.m., when it is hottest. Activity falls later in the day as it becomes cooler. Note that in the heavy rains this species is almost as numerous on the forest fringe as inside. In the case of *G. submorsitans* the numbers are too few, the community being dispersed throughout a huge area of open woodland ; activity would appear to remain fairly constant throughout the day.

Early Dry Season.—For *G. tachinoides* the cycle inside the forest is similar to that found in the rains, but now that the drier forest warms up more quickly, the period of great activity starts at 9 a.m. and lasts until 2 p.m. ; from then onwards activity within the forest decreases as the fly move out to the forest fringe (dotted curve). Note how, now that the rains are over, the disparity between the catches made in and outside the forest is increasing. The numbers of *G. submorsitans* are again too few, but activity appears to be maximal outside the forest at 9 a.m. and 3 p.m.

Cold Season.—*G. tachinoides* is completely inert within the forest until 9 a.m., when the weather becomes warmer ; activity then rapidly increases until 2 p.m. when the temperature is highest. Again, in the afternoon activity decreases inside the forest, being transferred to the margin of the wood. *G. submorsitans* is also inert on these cold mornings and does not appear on the fringe of the forest until 9 a.m. ; activity becomes maximal at 1 p.m., but then decreases as the fly move into the forest at 3 p.m., when possibly it is too hot for this species outside. Activity again becomes highest on the forest's edge at 5 p.m.

Hot Late Dry Season.—*G. tachinoides* entirely reverses its cycle ; activity is low at dawn, because the nights are still cold, but it rapidly rises to a maximum at 9 a.m. Then as the heat increases this species becomes inert on the forest's fringe between 11 a.m. and 4 p.m., and even within the forest the flies become very inactive. Activity increases greatly in the late afternoon. Note how few *G. tachinoides* are ever taken on the forest fringe in the hot weather. Now that concentration is complete, *G.*

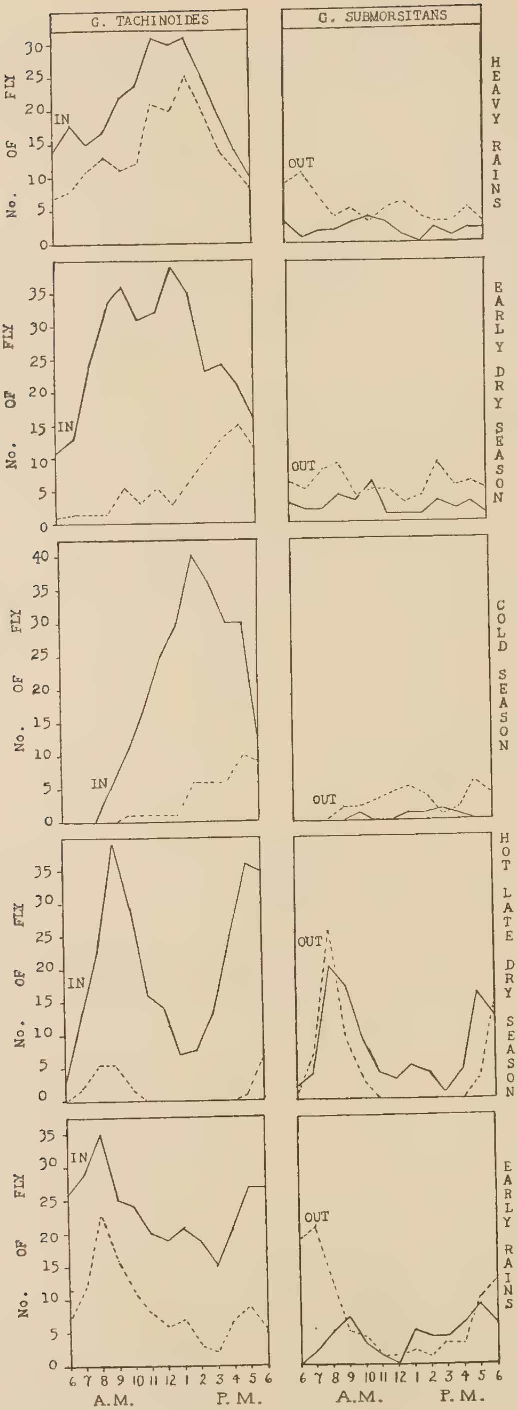

Fig. 4. Diurnal fly activity in the different seasons.

submorsitans is sufficiently numerous to give significant figures ; the diurnal activity cycle is similar to that described for *G. tachinoides*. Note that now *G. submorsitans* is commonest within the forest.

Early Rains.—The cycle for *G. tachinoides* is similar to that described for the hot season, but lower temperatures in the middle of the day produce a lesser degree of inactivity at this time ; fly never become entirely inactive, even on the forest fringe. The same remarks apply to *G. submorsitans*.

In order not to confuse the graphs given in fig. 4 the meteorological data were left out, but will now be dealt with in Tables X and XI.

In Table X all the temperature and activity data collected in the course of the experiment have been condensed by grouping temperature data into zones of 5°F., and by placing against each group the mean figure for all fly catches made when the temperature was within that group. It will be seen that both species are almost completely inactive between 46° and 60°F. ; above 60°F. activity increases, being high between 71° and 95°F., and maximal between 81° and 85°F. From 96° to 105°F. activity decreases rapidly, both species being completely inactive at temperatures above 105°F. ; hence both the lower and upper levels of the temperature range are inimical to the activity of both *G. tachinoides* and *G. submorsitans*.

TABLE X.

Relationship between Temperature and the Activity of G. tachinoides *and* G. submorsitans.

Temperature °F.	Average catch of *G. tachinoides*	Average catch of *G. submorsitans*	No. of observations.
46°–50°	0	0	3
51°–55°	0	0	4
56°–60°	1	0	8
61°–65°	4	2	9
66°–70°	8	4	17
71°–75°	12	4	44
76°–80°	16	5	51
81°–85°	18	6	50
86°–90°	15	5	61
91°–95°	11	5	57
96°–100°	9	4	32
101°–105°	6	2	39
106°–110°	0	0	5

From data that are too extensive to publish, further interesting results emerge. Along the forest edge both species are completely inactive at temperatures of 103°F. or over, whereas within the forest a few fly appear at 105°F., though activity is enormously reduced. The probable explanation is that along the exposed forest margin, even at ground-level, the temperature is still within the critical zone of 103°–106°F. (Nash 1935), so that tsetse evacuate the fringe and retreat into the forest ; but inside the true forest the surface soil temperature does not rise above 99°F., even though at four feet a whirling psychrometer may give a reading of 105°F. (Nash

1936a) ; hence a few very hungry fly may leave the safety of the soil surface and make a dart at a passing host, since short exposure to a temperature of 105°F. is not fatal (Buxton & Lewis, 1934, p. 180). In confirmation of this it is very striking to notice in the hottest hours tsetse settled at the base of tree-trunks within half an inch of the ground ; so sluggish are they that they do not fly until one has almost touched them.

Table XI is similar in construction to the previous table, but it deals with fly activity and saturation deficiency arranged in groups of 5 millibars. Clearly there is no well-defined relationship between fly activity and saturation deficiency ; fly are active even at the lowest readings, but it must be admitted that both species become entirely inactive with saturation deficiencies above 65 millibars ; since, however, such readings only occur when the temperature is exceedingly high, it is probable that temperature is the real cause of this inactivity.

TABLE XI.

Lack of Relationship between Saturation Deficiency and the Activity of G. tachinoides *and* G. submorsitans.

Saturation deficiency (millibars)	Average catch of *G. tachinoides*	Average catch of *G. submorsitans*	No. of observations
0–5	12	3	72
6–10	11	4	34
11–15	16	4	40
16–20	12	5	33
21–25	17	4	39
26–30	15	7	26
31–35	7	5	29
36–40	14	9	20
41–45	18	6	14
46–50	12	4	9
51–55	8	3	15
56–60	11	3	19
61–65	6	2	18
66–70	0	0	9
71–75	0	0	3

Morris (1934), working on *G. longipalpis* near Takoradi in the Gold Coast, has shown that activity is more closely related to temperature than to saturation deficiency, and that fly activity increases with rising temperature. He records no striking seasonal differences in the diurnal activity cycle, but then he was working in an equable coastal climate where the temperature range is much less then in Northern Nigeria.

In East Africa the writer tentatively suggested that " The weather must attain a certain degree of warmth and atmospheric dryness before *G. morsitans* will commence the day's activities ; the degree depends upon the season " (Nash 1933a). As admitted at the time, the data were meagre, and in view of the abundance of material upon which the present conclusions are based, the writer is doubtful whether " atmospheric dryness " did play a great part in the commencement of fly activity in Tanganyika.

Conclusions.

1. The diurnal fly activity cycle varies according to the season, the variations depending upon the temperature.
2. Both species are inactive between 45° and 60°F., and again at temperatures above 105°F. Activity is greatest between 81° and 85°F.
3. Tsetse avoid excessive high temperatures in the forest by becoming inactive near the ground-level.
4. Fly activity appears to be related to temperature, and not to saturation deficiency.

4. Fly Density as related to Season.

Owing to the extensiveness of the true habitats in East Africa and the enormous area in the fly-belt which permanently supports tsetse, the writer never attempted to produce figures purporting to represent the actual numbers of tsetse forming the community. The results published for the Tanganyika fly-round (Nash, 1933a) only attempted to give an index of the seasonal fluctuations in density ; this index depended upon the assumption that, if the fly-round path traverses the main vegetation types that represent the fly-belt, then fluctuations in the total fly caught along the whole length of the fly-round path will represent the fluctuations taking place in the whole community.

In Northern Nigeria the position is very different. Broadly speaking one can visualise the whole fly-belt that borders the Katagum River as being subdivided into a number of tsetse communities, each dependent upon its own particular strip of forest island, to which individuals in that area retreat in the hot season, and from which they spread out in the rains. It is not suggested that tsetse have a social instinct which confines them to their community, but rather that each strip of residual forest tends to have its own zone of influence.

In the community under investigation the path tapping the open woodland sections (I to V) can be pictured as one spoke of a wheel whose hub is composed of the residual forest, half of which is tapped by Sections VI and VII ; had it been practicable one could have had many other fly-round paths radiating out from the forest, tapping the surrounding open woodland, and representing the other spokes of the wheel.

Owing to the small size of the forest islands, Sections VI and VII are considered to tap quite half the concentration area for the whole community, whereas Sections I to V tap only a minute unknown fraction of the community's dispersal area. Thus in the late dry season, when the open country is almost evacuated, the numbers of tsetse caught in the half of the forest which is tapped indicate the size of about half of the total surviving tsetse community ; but at this season the figures for the open country continue to represent only an unknown fraction of the total community, as did the Tanganyika figures. In the late dry season the forest figures indicate the *actual* size of the community, whereas in the rains they represent only the *unknown fraction* of the total community that happens to remain in the forest. Since the forest figures mean two different things at two different times of the year, they can only be used with great caution to supplement the data given by the figures for the open country, which are considered to give a much truer index of seasonal fly density.

The data have been grouped under the five seasons of the year, and the average total catch for each season during three years is given in Table XII. This table is

TABLE XII.

Seasonal Fluctuations in the Population of G. submorsitans *in three Years.*

		Heavy rains : July, Aug. Sept.	Early dry season : Oct., Nov.	Cold season : Dec., Jan., Feb.	Late dry hot season : March, April	Early rains : May, June
The Open Country	Average seasonal fly density (true index)	163 Fly	106 Fly	39 Fly (activity)	35 Fly	115 Fly
	Average daily evaporation for the season	23 cc.	57 cc.	74 cc.	99 cc.	52cc.
	Mean percentage of total catch occurring in open country	63	50	41	15	24
The Forest	Average seasonal fly density (false index)	90 Fly	111 Fly	67 Fly (activity)	196 Fly	283 Fly
	Average daily evaporation for the season	6 cc.	22 cc.	34 cc.	48 cc.	28 cc.
	Mean percentage of total catch occurring in forest ...	37	50	59	85	76

divided into two ; the upper half gives the *true* index of the size of the population based on figures for the open woodland only, whereas the lower half supplies the *false* index, obtained from the forest figures—an index falsified by concentration. The average seasonal evaporation is given for both. Similarly the average seasonal percentage of the total fly-round catch that occurs in the open country, and the converse percentage for the forest, are also shown ; it must be remembered that these percentage figures, which indicate the expansion and contraction of the fly community, are ratios, and hence entirely independent of increases or decreases in fly density.

Reading from left to right, and studying the true index of fly density, it will be seen that fly are most numerous in the heavy rains, with an average density of 163 fly. As the dry season advances fly density decreases rapidly and becomes minimal in the hot months of March and April. (N.B.—The figure of 39 for the cold season is too low owing to the marked inactivity of tsetse in these months of dense haze and cold—catches made on the occasional bright day suggest that a figure of about 70 fly would be nearer to the truth.) In the early rains density rapidly increases. The third horizontal column shows that the tsetse community attains maximal dispersal when fly density is greatest ; this is the same as in Tanganyika.

Even though the forest figures are misleading when studying seasonal fly density, something can be learnt from them. In the heavy rains, when the forest is waterlogged, the density is low, because the forest has been partly evacuated in favour of the open woodland. As the evaporation rises to a favourable level in the early dry season the forest population increases, but there is still 50 per cent. of the community in the open country. By the cold season, increasing evaporation has led to a fall in density in both forest and open woodland, but the apparent fall is excessive owing to fly inactivity in these months.

In the late dry season, when the relative humidity in the open woodland may fall to 7 per cent. with a shade temperature reaching 110°F., the fly density is really at its lowest, but the numbers increase in the forest owing to the concentration of the few surviving fly from the open woodland. This is borne out by the percentage figures, which increase from 59 per cent. to 85 per cent. ; in this way a false impression of an increase in the fly population is created. To realize the utter falsity of this apparent increase, it must be recollected that the open country figure of 163 fly in the rains represented the density along only one spoke of the wheel. Were there 40 spokes, or were 40 fly-round paths sufficient to tap the open country, then 40 × 163 or 6,520 tsetse might appear to be the approximate size of the community. Hence, unless density does decrease in the dry season, some thousands of tsetse should be caught in the forest in the late dry season when concentration is complete ; but a mere 193 fly were taken—a matter of hundreds, not thousands. The relatively few tsetse that do find shelter in the true habitat must be regarded as a nucleus of survivors, which form the reservoir from which the great wet season population is evolved.

In the early rains the density in the forest increases from 196 to 283 fly, despite the fact that dispersal has already started ; since this increase is common to both forest and open woodland, there can be no doubt that the more equable conditions of this season result in a great increase in the size of the community.

When the writer was working in East Africa he found that the seasonal fluctuations in the size of the population were correlated with the fluctuations in the evaporation rate (Nash, 1933a and b) ; further, he found that a mean daily evaporation of 20–25 cc. formed an optimum zone for this species and that fly density decreased as evaporation rose or fell above or below this zone. Returning to Table XII, it will be noticed that the true fly density index was highest in the heavy rains, when the evaporation for the open country averaged 23 cc. ; again density was highest in the forest when the evaporation was 22 and 28 cc.—the early dry season and early rains respectively. Referring again to the true index it will be observed that density falls steadily as the evaporation rises and becomes minimal with 35 flies when the evaporation is maximal with 99 cc. This correlation between fly density and the evaporation rate is dealt with later on p. 122.

Fig. 5 is a diagram which has been constructed to summarise the data obtained in East and West Africa upon the seasonal fluctuations in the density of *G. morsitans*, and their relationship to the seasonal changes in the evaporative power of the air. The evaporation curves may be compared with safety, as both atmometers were exposed in similar open country. Note that in Nigeria the evaporation soars up so rapidly at the end of the rains that the period of high density is curtailed, whereas in Tanganyika the mild, damp conditions of the early dry season enable density to remain high until the end of the cold season in early August. Again note that the much longer Nigerian

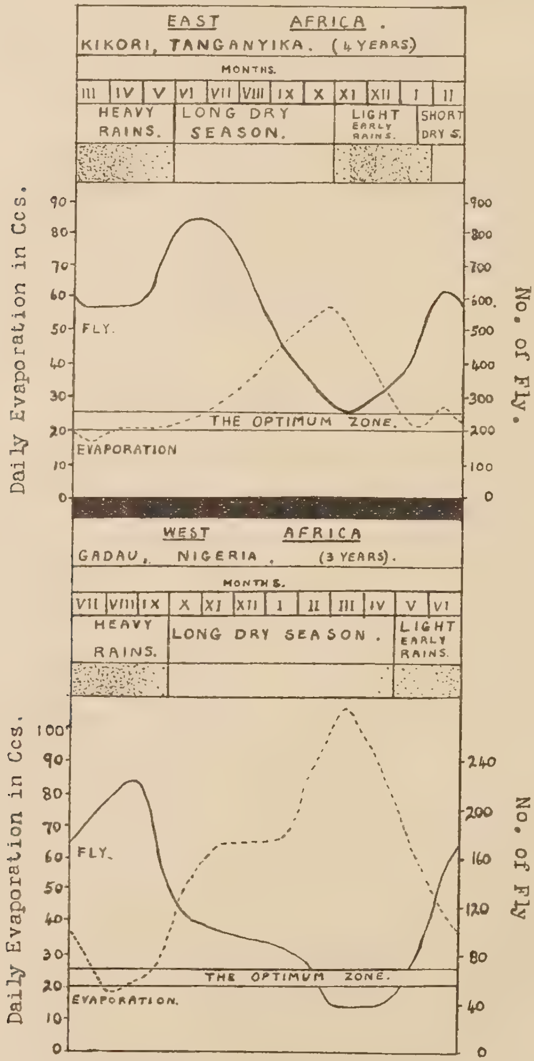

Fig. 5. The relationship between the seasonal density of *G. morsitans* and the evaporation, as found for East and West Africa.

dry season results in a longer period of fly scarcity, and that the evaporation only enters the optimum zone for a very short period in the year. Making allowances for these reactions to the local climate, one realizes that the general trend of the cycle is very similar in each case.

This resemblance in the cycle, despite the great climatic differences, convinces the writer that he has correctly elucidated the seasonal cycle for *G. morsitans*, and that those workers who have stated that this species is most numerous in the late dry season have been misled by local concentration, which they have mistaken for an increase in the population of the whole community.

It is interesting to note that in a recent paper Lloyd describes the seasonal cycle for *G. swynnertoni* in Tanganyika, and that his cycle is similar to that given by the writer for *G. morsitans* (Lloyd 1935, p. 453 ; Nash, 1933a). Possibly it will be found that this cycle, in relation to the local seasons, holds good throughout Africa for all species of tsetse that frequent open country.

No attempt is made to show the fluctuations in density of *G. tachinoides*, as it is impossible to obtain a true index for this forest tsetse ; however, judging from the figures and the breeding seasons, there is every reason to believe that its cycle is similar to that given for *G. submorsitans*.

Conclusions.

1. If tsetse concentrate excessively in a small area, the numbers of fly caught in that area will not furnish a true index of seasonal fly density ; such an index is best obtained from catches in the open woodland.
2. A daily evaporation of about 20 to 25 cc. a day would appear to afford optimum conditions for *G. submorsitans*.
3. Fly density is maximal in the heavy rains, when evaporation is near the optimum zone and dispersal is complete.
4. In the early dry season the soaring evaporation rapidly reduces fly density.
5. In the cold season evaporation steadies and the fall in density slows down.
6. The excessive evaporation of the late dry season results in minimal density.
7. During the early rains density rises steadily as the evaporation drops towards the optimum zone.
8. The seasonal cycle described and its relation to the evaporation are very similar to the results obtained for *G. morsitans* in Tanganyika.

5. Fly Longevity as related to Season.

This has already furnished the subject of a separate paper (Nash, 1936b). It was found for both species that as the maximum temperature rises so the longevity decreases, and that as the maximum temperature falls so longevity increases. Hence longevity is greatest in the rains and in the cold season, and lowest in the early and late dry seasons.

6. Duration of the Pupal Period as related to Season.

The influence of temperature upon the pupal period of *Glossina* is well known (Austen & Hegh, 1922 ; Newstead, 1924 ; Nash, 1933a). In the colder months of the year the pupal period increases, whereas it decreases in the warmer weather. In a laboratory investigation upon *G. submorsitans* and *G. tachinoides* at Gadau, Buxton & Lewis (1934) confirmed the fact that the duration of the pupal period depends upon temperature, and, further, they proved that humidity has no effect upon the period. The subject has been so thoroughly investigated that the writer will not give his results in detail ; however, he has found that the duration of the pupal period is closely related to the mean monthly temperature and that the duration of the pupal period averages 41 days in the cold season and only 19 days in the hot weather. In the cooler climate of Tanganyika the range for *G. morsitans* was between 53 and 29 days (Nash, 1933a).

The writer agrees with Buxton & Lewis (1934) that there is no evidence whatever to confirm the hypothesis of Pomeroy & Morris (1932, p. 515) that with *G. tachinoides* " the length of the pupal period is markedly affected by atmospheric humidity so that puparia deposited early in the dry season and those deposited late all appear to hatch out at about the same time, when rainfall causes an increase in atmospheric humidity."

7. Breeding-grounds and Breeding as related to Season.

Breeding-grounds of G. tachinoides *and* G. submorsitans.

In East Africa *G. morsitans* breeds freely in rock shelters when available, but the typical sites are under fallen trees in open woodland. The writer found that a trap, consisting of a log mounted on rollers and screened with bark, gave a much higher yield than any ordinary fallen tree (Nash, 1933a). At Gadau, in West Africa, similar traps were constructed, but it soon became apparent that *G. submorsitans* has adapted itself to the severer climate by breeding promiscuously upon the floor within thickets and forest islands ; the traps yielded very few puparia. On the eastern side of Lake Victoria Mr. H. M. Lloyd tried these traps against *G. palpalis*, but here again they were useless, because this species is also mainly a forest breeder. Log traps are clearly worthless except against a species of *Glossina* that breeds under fallen trees.

In West Africa the breeding-grounds of both *G. tachinoides* and *G. submorsitans* are constantly shifting, partly in relation to the seasonal dispersal and concentration of the adult population, and partly as the pregnant females move to areas which provide soil conditions suitable for the time of year.

The chief breeding-grounds of this district are as follows :—

Small Isolated Thickets.—Hundreds of these small thickets are found scattered throughout the woodland savannah ; they are built up around one or two trees which are overgrown and enshrouded with thorny creepers (Plate V, figs. 3, 4). They constitute the major breeding-ground for *G. submorsitans*, and are much used by *G. tachinoides* in the early dry season.

Residual Forest.—Relatively large patches of forest occur near the Katagum River, and throughout most of the dry season they are of great importance as breeding-grounds of *G. tachinoides* (Plate III, fig. 2 ; Plate V, fig. 1) ; they are utilised by *G. submorsitans* mainly in the late dry season.

Margin of River-bed.—In many stretches the banks of the Katagum River are fringed with a species of *Salix* (willow), which overhangs the margin of the sandy river-bed ; dense low shade is cast, and the sand though dry on the surface is moist at a depth of three inches (Plate V, fig. 5). This breeding-ground is not ready until the river margin becomes dry in February, but it becomes available just when most needed by the pregnant females of *G. tachinoides*, which find that in the hot season even the forest floor does not meet with their requirements. In May the river comes down in flood and this breeding-ground is destroyed.

Dry Season Breeding-grounds.

Evidence of the seasonal shifting of the breeding-centres of both species of tsetse was obtained from supervised puparia-rounds carried out in places selected as being typical of each of the three main types of breeding-ground ; at regular intervals throughout the dry season four skilled boys searched each area for six hours.

The average monthly yield of *G. tachinoides* puparia for each type of breeding-ground is given in Table XIII. In addition the mean monthly evaporation and temperature at four feet above ground-level are given in the last columns ; these figures are not strictly relevant, as they were taken in a different forest island and not at the level of the soil, but they should indicate the drying up process that takes place within both thickets and forests as the dry season advances.

TABLE XIII.

Average Monthly Returns of G. tachinoides *Puparia.*

Season	Month	Small thickets	Residual forest	Margin of river-bed	Mean monthly forest evap. cc.	temp. °F.
Early dry season	Oct.	30	45	Contained water	18	77
	Nov.	188	166	,,	26	72
Cold Season	Dec.	112	303	,,	27	69
	Jan.	58	300	,,	29	67
Hot dry Season	Feb.	22	110	292	39	76
	March	0	35	466	50	83
	April	1	17	224	42	84

The writer interprets the figures in Table XIII as follows :—Breeding in the innumerable small thickets is widespread in November, but rapidly increasing evaporation causes a movement into the larger and damper forest islands, where breeding remains centred until evaporation soars up in February ; the pregnant females then shift again and practically confine their attentions to the damp sand of the river-bed. In places where the forests are remote from the river, reduced breeding continues within them, but probably pupal mortality is high.

The continuous shifting of the breeding-grounds coincides with steadily rising evaporation, not with temperature, which falls from October to January and rises from February to April. This might suggest that the movement of the breeding-grounds follows the concentration of the adult population, which, as shown on p. 88, is related to rising evaporation ; however, this can only be partly true, because when breeding shifts from the forest to the sand river the fly community does not move *en masse* to the river, but remains concentrated in the forest.

Probably at high temperatures the choice of breeding-grounds depends upon the sensitiveness of the pregnant females to the humidity conditions of the soil, since suitable humidity is essential to the health of *G. tachinoides* puparia. Buxton & Lewis (1934, p. 216) showed that though actual submergence of the puparia caused death, yet at high temperatures a high degree of humidity is essential to a high rate of emergence. With the temperature constant at 86°F., a 98 per cent. relative humidity resulted in a 92 per cent. emergence, but as humidity dropped so emergence decreased until at 11 per cent. humidity only 13 per cent. of the puparia emerged ; at the lower temperature of 75°F., the optimum humidity was lower, an 88 per cent. humidity giving 100 per cent. emergence. Certainly the shifting of the breeding-areas from small thickets to dense forest and thence to the moist river sand suggests that, as evaporation rises, the females seek out those places in which the soil retains some moisture.

The writer has had many breeding localities under observation and has noticed that, even when dealing with one class such as small thickets, there is a great individual variation in the month when each attains its maximum popularity. The attractiveness of a thicket cannot depend upon general atmospheric meteorological conditions, but upon microclimatic conditions within that thicket.

Between February and May all puparia kept in the laboratory, or in an open grass hut under the heavy shade of a tree, produced 100 per cent. mortality, thus wrecking the writer's experiments on seasonal viability ; it was found that puparia had to be kept within a meat-safe covered with wet sacking, when 60 per cent. emergence could be obtained. Clearly puparia in the field can only survive this season owing to the cooler and damper conditions within the soil.

Figures comparable to those given in the previous table are shown for *G. submorsitans* in Table XIV ; the puparia were collected in the same sites and at the same time.

TABLE XIV.

Average Monthly Returns of G. submorsitans *Puparia.*

Season	Month	Small thickets	Residual forest	Margin of river-bed	Mean monthly forest	
					evap. cc.	temp. °F.
Early dry season	Oct.	3	0	Contained water	18	77
	Nov.	49	8	,,	26	72
Cold season	Dec.	56	4	,,	27	69
	Jan.	47	7	,,	29	67
Hot dry season	Feb.	22	12	0	39	76
	March	19	35	8	50	83
	April	26	61	8	42	84

It will be seen that *G. submorsitans* does not start breeding until November, which is about three weeks later than *G. tachinoides*. *G. submorsitans* breeds almost exclusively in small thickets until the beginning of the hot season, when much of the breeding shifts into the forest, but breeding never ceases in the thickets, nor does the river-bed ever play an active part in the reproduction of this species.

G. submorsitans is less exacting than *G. tachinoides* in its breeding requirements, probably because its puparia are more resistant to high temperature and low humidity. Buxton & Lewis (1934, p. 214) showed that at a constant temperature of 86°F. an emergence of over 70 per cent. for *G. tachinoides* could only be obtained if the relative humidity was over 88 per cent. ; whereas a 77 per cent. emergence of *G. submorsitans* could be obtained even at 19 per cent. humidity.

The difficulty of eradicating *G. submorsitans* is illustrated by its lack of dependence upon the easily cleared forest islands and the riverine strip of willow, and further by its ability to breed in the countless thickets, even in the hottest weather ; facts which confirm the writer in his opinion that it is economically unsound to attempt anti-tsetse clearing measures against this species when there are so many urgent problems in which *G. tachinoides* alone is involved.

Wet Season Breeding-grounds.

The margin of the river-bed becomes less attractive to *G. tachinoides* in the early rains because the sand becomes sodden—a prelude to the river coming down in flood in mid-May. This species breeds to a reduced extent inside the forest islands throughout May, but in June and July no puparia can be found within these breeding-grounds—a fact which made the earlier workers conclude that *G. tachinoides* and *G.*

submorsitans ceased breeding in May or early June. Actually, *G. tachinoides* continues to reproduce until the end of July, but it has shifted its breeding from inside the forest to exposed sites under tall trees on the forest's edge ; such sites are accessible to the sun except around mid-day, and support herbaceous growth.

G. submorsitans breeds to a reduced extent in the forest islands and small thickets throughout May ; it then evacuates these sites and throughout June and July breeds exclusively under logs in the woodland savannah ; for this short period only can *G. submorsitans* breed in the typical *G. morsitans* sites of East Africa.

Breeding as related to Season.

In West Africa it is difficult to discover the exact time of year when breeding throughout the tsetse community is maximal, because each type of breeding-ground has its own season of maximum popularity, depending upon when it becomes most attractive to the pregnant females. Thus breeding by *G. tachinoides* is maximal in small thickets in the early dry season, in residual forest in the mid-dry season, and in river-bed in the late dry season.

Should we combine the figures from all breeding-grounds and plot the monthly returns (as did Taylor, 1932), we should be bound to find that breeding was greatest in the late dry season, simply because breeding is then concentrated in small areas, enabling the searchers to find hundreds of puparia daily ; it is easier to find a needle in a bundle of hay than in a hay-stack. The deception due to pupal concentration was accentuated in Taylor's graph because he did not have the small isolated thickets searched, as he did not realise their importance ; the results was that his early dry season figures were far too low, relative to his late dry season totals.

So far it is safe to conclude that both species breed extensively throughout the dry season, and to a decreasing extent throughout the early rains and up till the end of July.

In August and September the soil is never dry enough to make searching for puparia even a possibility, so in order to obtain information about this period it was decided to provide a small area of dry humus on the margin of the forest. A grass hut was built 14 feet long by 11 feet wide ; the roof was covered with a tarpaulin and the eaves extended to within 15 inches of the ground (Plate V, fig. 6) ; a drainage trench was dug beneath the eaves and it was found that the soil within remained permanently dry. The hut immediately proved attractive, especially to *G. tachinoides*, so that it became possible to study breeding throughout the year with a certainty that the results would not be masked in the rains by the inability of the searchers to detect the puparia. At monthly intervals six boys spent two consecutive days combing the floor of the hut for every puparium. The average monthly yield for the rainy season over a period of two years is given in Table XV.

TABLE XV.

The Mean Monthly Numbers of Puparia in the Hut, and Rainfall, over Two Years.

Months	Rainfall inches	*G. tachinoides* puparia	*G. submorsitans* puparia
May ...	2·0	17	19
June ...	3·4	23	3
July ...	5·8	15	2
Aug. ...	11·2	0	0
Sept. ...	4·7	21	0
Oct. ...	0·2	106	1

The females of *G. tachinoides* within the forest appear capable of successful pregnancy throughout all months of the rains except August, when the rainfall is highest ; owing to a possible concentration of larviposition in the only dry soil available, the number of puparia found in these 154 square feet of forest floor may be larger than elsewhere, but even so, the existence of the hut cannot be held responsible for the females becoming pregnant, and hence, had there been no hut, these females would undoubtedly have had to extrude their larvae somewhere ; it is thus evident that *G. tachinoides* does breed and produce puparia in all months of the rains except August, when the atmosphere is almost saturated.

The hut was never attractive to *G. submorsitans*, which prefers small thickets to the forest, and the decreased yield in June probably indicates that this species was then breeding under logs in the savannah woodland ; however, the figures suggest that reproduction ceases until the end of September, and this is in keeping with the results obtained elsewhere, which showed that this species is later than *G. tachinoides* in recommencing breeding.

Instead of using the actual, but fallacious, figures derived from the monthly puparia returns for all breeding-grounds combined, the writer prefers to construct a diagram to illustrate breeding as related to season ; this diagram is the result of a careful scrutiny of all available data drawn from puparia-rounds, the puparia hut, and from pregnant female and young fly percentages. The average monthly rainfall over 6 years is also given (fig. 6).

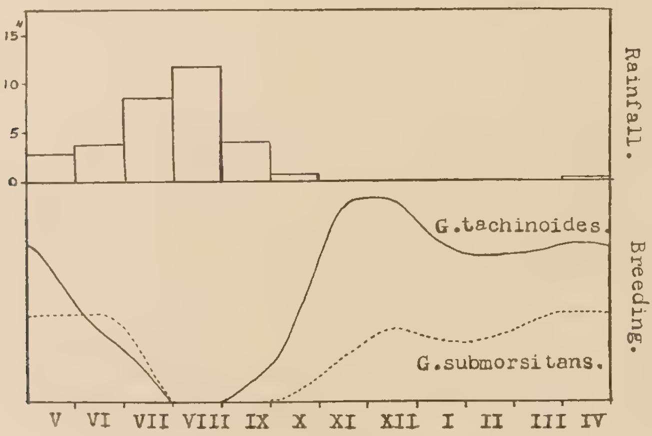

Fig. 6. Diagram of seasonal breeding-cycle.

It will be seen that *G. tachinoides* ceases to breed in the heavy rains for one month, and *G. submorsitans* probably for two, but otherwise breeding continues throughout the whole year. *G. tachinoides* undoubtedly breeds extensively at the end of the rains and continues breeding at a high though somewhat reduced rate right through the dry season, and only slackens off in the early rains. *G. submorsitans* behaves similarly, though it starts later and continues breeding further on through the following rains ; however, this species does not breed so extensively in the first half of the dry season, and probably reproduces most after the first storm in April.

Both species must be able to breed throughout a great range of climatic conditions, since neither the cold and haze of December and January, nor the great heat and evaporation of March and April, seem capable of seriously interfering with breeding ;

only the saturated atmosphere of the heavy rains arrests the reproductivity of the female. In the forest a mean relative humidity of 95 per cent. at a mean temperature of 73·5°F. was recorded for the last fortnight of August 1935 ; even in the open exposed meadow-pan the mean humidity for a fortnight has been 87 per cent. at 77°F. It cannot be low temperature that is the cause of this cessation of breeding, as the temperature is much lower in the cold dry season when reproduction is considerable ; it would appear that very high humidity and low evaporation are definitely inimical to breeding.

The Breeding-Cycle as related to Fly Density.

It may have been remarked that breeding is greatest in the dry season when fly density has been shown to be decreasing, and that in the early rains when breeding decreases, fly density is increasing. The following explanations are suggested :—

1. When *G. tachinoides* breeds in widely scattered thickets at the end of the rains the climate in the open woodland is favourable for the parents, but by the time the offspring have emerged the climate is adverse, and probably the bulk of the progeny die before they can find a forest sanctuary.
2. In the cold season the great prolongation of the pupal period may cause a high pupal mortality owing to the normal loss of water (due to evaporation from the puparium) being continued for an abnormally long period (Buxton & Lewis, 1934, p. 220).
3. In March, high temperature probably causes a high pupal mortality in the forest, since Buxton & Lewis (1934, p. 214) showed that the emergence percentage for *G. tachinoides* is much higher at 75°F. than at 86°F. ; in the late dry season of 1935 the writer found that even under logs in the densest forest the average surface soil maximum temperature over 52 days was 93°F., with an absolute maximum of 99°F. (Nash, 1936a). Again, adult longevity is lowest in the late dry season (Nash, 1936b) ; hence, if pupal mortality is also high, as stated by Taylor (1932) and Chorley (1929), there is abundant cause for the minimal fly density of that season.
4. In the dry season much of the breeding is probably wasted effort, but it is believed that, as soon as the early rains break, increased pupal viability (Taylor, 1932) and improving climatic conditions for the adults enable the population to increase, despite a breeding rate that is lower than in the dry season.

The subject is dealt with further on pp. 115–116.

It has recently been found that inside thickets *G. submorsitans* breeds to a considerable extent in rot-holes situated about one foot above the surface of the soil ; *G. tachinoides* puparia have never been found in these sites.

8. Favourable and Unfavourable Climatic Conditions for G. submorsitans and G. tachinoides.

Hitherto the different reactions of the fly community to changing seasons have been elucidated, and the meteorological factor which is primarily responsible for controlling each type of reaction has been indicated (*e.g.*, longevity is primarily controlled by temperature). An attempt will now be made to show what sets of meteorological conditions result in optimum and adverse fly conditions.

During these years, the month in each year in which each fly factor (density, dispersal, etc.) became maximal was written down, together with all the meteorological data for that month and the previous month. By taking the average for the three years, mean optimum meteorological figures were obtained for that month and the previous month, but the mean for these two months has been taken as giving the final figure, because the period between climatic change and resultant fly reaction is uncertain. Such final figures have been worked out for each fly factor for both species of tsetse, and similar data have been produced to represent the most adverse climatic conditions. The data are far too extensive to present in this form, but an example is given in Table XVI, which shows optimum conditions for *G. submorsitans* only.

TABLE XVI.

Optimum Meteorological Conditions for the Dispersal, Density, and Longevity of G. submorsitans.

Meteorological factors (average for same and previous months)	Maximum dispersal	Maximum density	Maximum longevity
Mean rainfall	8·8 in.	9·1 in.	12·7 in.
Mean evaporaton	22cc.	22 cc.	25 cc.
Mean saturation deficiency	6·8 mb.	7·0 mb.	7·5 mb.
Mean temperature	78·9°F.	79·0°F.	79·5°F.
Mean maximum temperature	88·1°F.	87·9°F.	91·9°F.
Mean minimum temperature	73·0°F.	73·1°F.	74·0°F.
Mean range	15·1°F.	14·8°F.	17·9°F.

It will be seen that maximal dispersal, density, and longevity, occur under very similar climatic conditions, but this is only to be expected, as each of these fly factors always becomes maximal at some time during the heavy rains. It also happens that these fly factors all give minimal figures in the late dry season, under almost identical climatic conditions, so that it has been possible to compress the data still further by taking the average of these meteorological figures, giving one set of conditions that is applicable to this group of fly factors (Table XVII).

In Table XVII all the data are summarised, so as to give a general idea of the type of climate that locally proves optimum, adverse, and insupportable to the different activities of the tsetse community.

Optimum Conditions.—In the first column, the data representing the ideal climatic conditions have been taken from the Meadow-Pan Station ; this is sound, because up to 90 per cent. of the total population of *G. submorsitans* is dispersed throughout the open country at this time. Such a climate does not afford ideal conditions for the dispersal of *G. tachinoides*, since dispersal though maximal is on a very small scale, but it does indicate the best conditions available in this part of Nigeria ; further south, higher humidity may result in a greater wet season expansion.

In the second column the ideal conditions for *G. tachinoides* are given ; these figures are taken from the Forest Station, as even at this season from 80 per cent. to 90 per cent. of the population occurs within the residual forest. The optimum figures for *G. tachinoides* indicate that this species prefers a higher humidity and lower temperature than *G. submorsitans.*

In the third column the data are taken from the Forest Station, because pregnant females tend to lead a life of inactivity in dense shade, where they finally extrude their larvae. The figures are for November and December when *G. tachinoides* breeds extensively and *G. submorsitans* considerably, but since both species can breed over a tremendous climatic range the figures merely represent a set of meteorological conditions which should result in successful reproduction, if reproduced artificially in the laboratory.

TABLE XVII.

Favourable and Unfavourable Climatic Conditions for G. submorsitans *and* G. tachinoides.

Meteorological factors (Average of monthly figures for same and previous months)	Optimum conditions for			Adverse conditions for density and longevity of both species (Forest Sta.)	Insupportable conditions for	
	Density and longevity of *G. submorsitans*, also for dispersal of both species (Meadow-Pan Sta.)	Density and longevity of *G. tachinoides* (Forest Sta.)	Breeding by *G. tachinoides* and also favourable for *G. submorsitans* (Forest Sta.)		All functions of both species (Meadow-Pan Sta.)	Breeding by both species (Forest Sta.)
Total rainfall ...	10·0 in.	9·0 in.	0·0 in.	0·2 in.	0·0 in.	14·0 in.
Mean evaporation ...	23 cc.	8 cc.	27 cc.	50 cc.	115 cc.	4 cc.
Mean sat. def. ...	7 mb. (5 mm.)	4 mb. (3 mm.)	11 mb. (8 mm.)	25 mb. (19 mm.)	29 mb. (22 mm.)	3 mb. (2 mm.)
Mean temperature ...	79°F. (26·1°C.)	77°F. (25·0°C.)	71°F. (21·7°C.)	85°F. (29·4°C.)	85°F. (29·4°C.)	75°F. (23·9°C.)
Mean maximum temp.	89°F. (31·7°C.)	84°F. (28·9°C.)	86°F. (30·0°C.)	99°F. (37·2°C.)	102°F. (38·9°C.)	80°F. (26·7°C.)
Mean minimum temp.	73°F. (22·8°C.)	73°F. (22·8°C.)	57°F. (13·9°C.)	71°F. (21·7°C.)	67°F. (19·4°C.)	72°F. (22·2°C.)
Mean range (Mean maximum — mean minimum temp.)	16°F. (8·9°C.)	11°F. (6·1°C.)	19°F. (16·1°C.)	28°F. (15·5°C.)	35°F. (19·5°C.)	8°F. (4·5°C.)

Adverse Conditions.—In the late dry season the open country is evacuated by *G. tachinoides* and *G. submorsitans*, both species concentrating in the forest, where they manage to survive but do not prosper ; hence forest readings for this season should indicate climatic conditions approaching the fatal limit.

Insupportable Conditions.—At the end of the dry season the meteorological conditions in the Meadow-Pan Stations are presumably insupportable to the fly. The temperature frequently rises above the upper fatal limit, and fly kept in dense shade in such country often die on the same day ; even the savannah woodland surrounding the forest fringe is evacuated by tsetse from 11 a.m. to 4 p.m. Hence the figures in the first column represent a set of meteorological conditions that are considered fatal to both species. A set of conditions is given in the last column which is believed to be capable of arresting the reproduction of both species.

Table XVII should throw light upon the seasonal abundance of *G. submorsitans* and *G. tachinoides*, and also upon their local and geographical distribution ; further it should be of value to laboratory workers. For example, Buxton & Lewis (1934) had no field data to guide them in their choice of temperature and so carried out most of their experiments upon the effect of different humidities upon fly longevity, reproduction, etc., in incubators kept at 86°F. This temperature was definitely too high, as such a mean monthly temperature would only be recorded in the field at the season which is most unfavourable to both species.

Conclusions.

1. Excessive evaporation, high maximum temperature and a great diurnal temperature range are inimical to high fly density.
2. A constant temperature of 79°F. with a saturation deficiency of 7 millibars provides optimum conditions for *G. submorsitans* at Gadau*; a saturation deficiency of 11 millibars probably increases the breeding rate.
3. A constant temperature of 77°F. with a saturation deficiency of 4 millibars provides optimum conditions for *G. tachinoides* ; a saturation deficiency of 11 millibars probably increases the breeding rate.

THE FOOD FACTOR.

1. The Fauna and its Seasonal Distribution.

In the Gadau area game is plentiful in the fly-belt during the cold and late dry seasons, but in the heavy rains it moves away from the low-lying tsetse bush to the well-drained sand-ridges.

G. submorsitans succeeds in following the game to the adjacent sand-ridges, and individuals have been caught as far as six miles from the nearest residual forest, but only in August when the rains are heaviest ; *G. tachinoides* is incapable of any large-scale spread into open country, and merely extends into small thickets in the river plain. The seasonal distribution of host animals which occurs in the fly-belt can be summarised as follows :—

1. Residual Forest : Bushbuck, monkeys and a few wart-hog can be found all the year round in these small forest islands, which being elevated, are never inundated during the heavy rains.
2. Meadow-Pan and Woodland Savannah : Game is almost non-existent during the heavy rains (July and August) when this country becomes flooded. Game continues to be scarce in the early dry season, but for ten months in the year the following species are to be found : Man, wart-hog, red-fronted gazelle, reedbuck, oribi, duiker and waterbuck ; these are abundant in the late dry season and early rains—February to June inclusive.

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* These conditions are the best available locally, but Gadau is considered to be near the hot, dry limit of the range of the species. Probably a saturation deficiency of 6 millibars at 73°F. would be even more favourable (see p. 123).

Herds of Senegal hartebeest and roan antelope are also common in the fly-belt, but only for some five months in the year. They start entering the fly-belt in February, having deserted the further sand-ridges in favour of country nearer the river ; some of these herds have probably migrated from a long distance. During June when the black clay of the meadow-pan is becoming very heavy for walking, the last of these herds leave the fly-belt and retreat into the thick and extensive savannah woodland of the higher sand-ridges, where they stay throughout the heavy rains, early dry, and cold seasons, reappearing in the river-plain in February.

To summarise, it can be said that hosts for the tsetse only appear to be scarce in the heavy rains—July and August ; they become more plentiful from September to January and abundant from February to June.

The data given above have been obtained from the records of fresh spoor and game seen on the fly-round, but it is more satisfactory to estimate the seasonal fluctuations in the food factor from a study of the state of nutrition of the sample catches that are made four times in each month.

2. Diagnosis of the State of Adult Nutrition.

During the three years in which the fly-round has been in existence the degree of hunger among the flies caught has been estimated from their external appearances. Only old male flies are employed ; females are ignored, because of the complications produced when they are pregnant, and also freshly emerged flies, because they are always hungry on hatching. All the existing work upon the estimation of hunger from external appearances has been done by Dr. Jackson, who in 1930 recognised five stages of hunger, which in 1933 he reduced to four.

The writer recognises only three stages of hunger, and only two of them are subsequently employed :—

Gorged : When viewed externally the centre of the abdomen is red or black with ingested blood. If no blood can be plainly seen in the centre, but the sternites appear black, then the fly is graded as intermediate.

Intermediate : All flies that are in neither of the extreme stages are grouped as intermediate.

Starved : The test for this stage is to hold up the fly against the light by its head and then look at the ventral surface (a suggestion of Mr. Swynnerton's). If the fly is hungry its abdomen will be relatively empty, and hence the degree of hunger can be gauged by the size of the area that appears translucent against the light. The fly is only considered starved when the translucent area begins at the anterior end of the abdomen and extends backwards to the beginning of the fifth abdominal segment, which is clearly demarcated by the anterior edge of the two dark chitinous plates or hectors (Hegh 1929, p. 237), which lie immediately in front of the hypopygium.

Intermediate flies are not considered of any use as an index of hunger, so that attention can be confined to the other two stages. As only 2–3 per cent. of the fly caught in this fly-belt are starved, the percentage of old males that are gorged is used as the hunger index.

3. Seasonal Nutrition.

In fig. 7 the mean monthly percentage of gorged flies among old males has been plotted for both species. It will be seen that *G. tachinoides* (dotted curve) is a much better fed species that *G. submorsitans* ; this is to be expected, since *G. tachinoides* is much less specialised in its diet and takes both reptilian and mammalian blood without hesitation (Lloyd, Johnson, Young & Morrison, 1924). There is a great similarity between the seasonal fluctuations in hunger which both species exhibit.

In the late dry season and the early rains (March to May) tsetse are best fed ; at this season game and tsetse are concentrated near the river where the residual forest islands offer them both shade during the heat of the day.

As the rains increase the game tend to evacuate the fly-belt for the higher sand-ridges. *G. submorsitans* attempts to follow the game, but it must have great difficulty in finding its hosts in such extensive areas of thick woodland and very high grass. The dispersal and consequent reduction in the size of the mammalian food supply on the fly-round is reflected by the steady decrease in the percentage of gorged fly throughout June, July and August. This increased hunger is not so evident in the case of *G. tachinoides*, which is not forced to keep in touch with the game, being able to revert to the abundant reptilian life of the wet season. (Lloyd & Johnson, 1924, showed that *G. tachinoides* takes much more reptilian blood in the rains.)

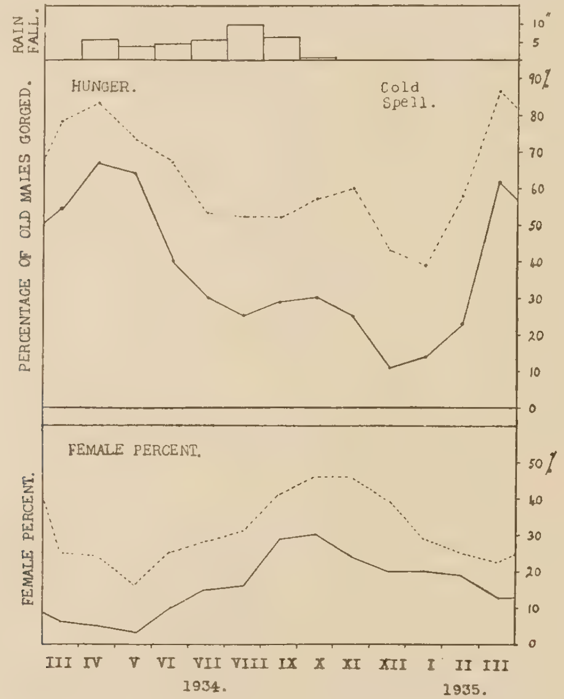

Fig. 7. Seasonal variations in the hunger of old males and in the percentage of females that attack man. (*G. tachinoides*—dotted curve ; *G. submorsitans*—solid curve.)

At the end of the rains there is a slight tendency for fly to be better fed, but the grass is still unburnt and hosts are hard to find. In December the combination of cold weather, dense haze and overcast conditions, greatly reduces the activity of fly and hence the number of hours during which they can hunt ; this results in a period of maximal hunger, which however cannot be sufficiently pronounced to affect the community adversely, since longevity is greatest at this season (Nash, 1936b).

In February and March the weather becomes very hot, the grass has nearly all been burnt, and much game congregates near the residual forests where the fly are concentrated ; once more the fly are mostly gorged.

The data given are only for 13 months, but similar results have been obtained over a period of 3 years. Lloyd, Johnson, etc. (1923 and 1924), using different methods, also concluded that flies were better fed in the dry season than in the rains, but they did not mention the maximum hunger of the cold spell.

These Nigerian results agree with those of Mr. Chorley working on *G. palpalis* in Uganda, but are the exact opposite to Dr. Jackson's results in Tanganyika Territory, where he finds that *Glossina morsitans, swynnertoni* and *pallidipes* are all much hungrier in the dry season than in the rains—a fact that he attributes to the effect of low humidity, which greatly hastens the onset of hunger (Jackson, 1933).

The writer believes that these anomalies in seasonal nutrition are entirely due to local conditions. If conditions are such that during the rains food becomes very scarce owing to long grass, floods, and the consequent evacuation of the fly-belt by game, then, even though tsetse can go for longer periods without food, they are bound to become hungry. Similarly, in the dry season, if game and tsetse concentrate in the same small areas fly are certain to be well fed, despite the necessity for more frequent meals.

4. The Effect of Hunger upon the Female Percentage.

Seasonal fluctuations in the female percentage are shown in the lower half of fig. 7. Comparing these curves with those shown above for hunger, one can say that the female percentage is lowest (*i.e.*, that females attack man most rarely) when food is most abundant in March, April and May (late dry season) ; but when fly are hungry between August and January the females attack man more readily, resulting in high percentages of females in the catches. One might have expected the female percentage to be maximal in the cold spell when the community is hungriest, but this is probably prevented by abnormal female inactivity caused by low temperature.

Generalising, one can say that females of both species only attack man in large numbers when the tsetse community shows signs of hunger, suggesting that hunger makes them overcome their dislike for human blood.

TABLE XVIII.

Summary of Data collected from 3½ Miles of Fly-Round over 2 Years (27.v.33–23.v.35).

Species	Total fly caught	♀%	Hunger, using old ♂s only		
			Total	Gorged %	Starved %
G. tachinoides ...	17,011	30	10,621	65	3
G. submorsitans ...	30,618	11	24,865	45	2

It will have been observed in fig. 7 that female *G. tachinoides* always attack man more readily than female *G. submorsitans* ; this fact is more apparent in Table XVIII, based on the summarised fly-round statistics for two years. Whereas 30 per cent. of the total catch of *G. tachinoides* were females, only 11 per cent. of *G. submorsitans* belonged to this sex ; yet the sexes of both species emerge from puparia collected in the bush in almost equal numbers, so that 50 per cent. females would be possible in a catch. The probable explanation is that whereas human blood may be slightly distasteful to *G. tachinoides* females, it is definitely very unattractive to *G. submorsitans* females, so that they do not appear to man in their true numbers unless overcome by excessive hunger. Johnson & Lloyd (1923, p. 381) reached the same conclusions. In confirmation of this the writer has frequently observed colonies of *G. tachinoides* thriving in places surrounded by cultivation, where man must form the bulk of their diet, but *G. submorsitans* is never found unless wild game is abundant, which means that the human population is scanty.

The data for hunger in Table XVIII confirm fig. 7, which showed that *G. tachinoides* is always the better fed species. Starved fly of either species are very rare in this fly-belt.

THE VEGETATION FACTOR.

1. The Vegetation Units.

For the purpose of studying the ecology of *Glossina*, the writer considers that the vegetation communities of this fly-belt can be grouped under three heads :—

Residual Forest.

Such forest is a relic of Closed Forest and takes the form of riverine strips of forest islands surrounded by savannah woodland. A patch of this residual forest is rarely a homogeneous unit, as it is usually built up out of clumps of true forest cemented into a whole by a wind-break of protective, peripheral thicket, which intrudes into the forest in tongues, wherever there is an absence of high shade.

In this area there are two local dominants in the true forest—stands of tall, thin, straight-trunked *Diospyros mespiliformis* (ebony tree), and isolated *Celtis integrifolia* with large girths and buttressed roots (Plate III, fig. 2). The crowns of these forest trees are united by lianes to form a high canopy which permits only dappled sunlight to reach the rich humus floor, which is almost free from herbaceous undergrowth.

In sharp distinction is the " intrusive thicket " of *Dichrostachyis platycarpa*—a huge impenetrable bramble, which chokes the forest glades, and billows upwards to great heights near the edges where it can obtain support from the bordering trees. Seen from without the forest, it appears as a light green spider's web slung across a gap in the wall of dark-foliaged trees, but from within it appears as a tangled skein of woody, leafless, intertwining stems, that bar further progress.

Woodland Savannah.

This vegetation type exists over large areas of country and clothes the extensive sand-ridges which separate series of shallow drainage depressions or meadow-pans. The woodland is composed of many species of trees, the commonest being *Bombax buonopezense* (red-flowering cotton tree), *Anogeissus schimperi*, *Terminalia* spp., and *Combretum* spp. *Hyphaene thebaica* (dum palm) is a common local dominant. The only large timber trees are *Pterocarpus erinaceus* and *Khaya senegalensis.* In the rains the grass is at least ten feet in height and visibility is very poor ; this grass does not burn cleanly and even after the fires the visibility is not very great (Plate V, fig. 2). Owing to insufficiency of shade in the late dry season, woodland savannah cannot permanently support a tsetse population, but providing there is some residual forest within a few miles which can act as a reservoir, this woodland becomes re-colonised annually during the rains ; breeding takes place when small thickets of vestigial forest occur amid the woodland savannah, which thus frequently acts as a temporary habitat until it is evacuated in February.

Meadow-pan.

The writer has coined this term in order to avoid bringing further native names into the literature upon *Glossina.* " Meadow-pan " is identical with the " fadama " and " fako " of Northern Nigeria, the " mbuga " of East Africa, and the " vlei " of Rhodesia and South Africa. The vegetation type is sparse tree-growth with expanses of pure grassland in the depressions ; the appearance of the latter in the rains gives the general impression of swampy meadow-land, while in the dry season the whole formation becomes an open expanse of pan with hard, cracking, black-cotton soil from which the grass has usually been entirely destroyed by fire. The term " meadow-pan " therefore expresses the two entirely different seasonal appearances of this formation (Plate IV, figs. 1, 2).

At Gadau the tree growth of the formation is represented by the " Baobab and Thorn " of Lloyd, Lester, Taylor & Thornewill (1933), which supports such species as *Adansonia digitata*, *Zizyphus jujuba*, *Balanites aegyptiaca*, *Albizzia chevalieri* and *Acacia seyal*, *A. senegal*, and *A. siberiana*. A common feature is the solitary *Tamarindus indica*, which, smothered in *Dichrostachys platycarpa* and other xerophytic lianes, forms a small thicket. With the exception of occasional *Mitragyna africana*, the centre of the meadow-pan is usually treeless ; in the rains the depression becomes flooded, forming a slow-moving sheet of water that drains into the large Katagum River. Both the fringing baobab and thorn and the central depression are included in the term " meadow-pan," as the typical black-cotton soil is common to both, the only difference being that the more extensive flooding of the centre of the pan tends to preclude the growth of trees, owing to the greater acidity of the soil.

Meadow-pan, like woodland savannah, can only support tsetse during and just after the rains ; it cannot be classed as a temporary habitat because the hard clay makes breeding impossible during the dry season, and in the rains it is inundated. It is similar to a modified East African feeding-ground in mbuga or hard-pan.

2. The Distribution within the Vegetation of the Elements composing a Fly Community.

The data upon this subject have been given in Table XIX and have been obtained from the fly-round figures for the last two years. Each species will be dealt with separately, and fly density will be expressed as " Flies, per boy, per 100 yards." (Nash 1930, p. 208).

G. tachinoides.—In meadow-pan and woodland savannah the fly density is exceedingly low and the female percentage very high ; where a road passes through the woodland the flies are much better fed, though there is no suggestion of a path concentration. On the fringe of the residual forest *G. tachinoides* are more numerous, better fed, and the female percentage lower.

TABLE XIX.

Analysis of the Vegetation Preferences exhibited by G. tachinoides *and* G. submorsitans *Communities*

G. tachinoides			Nature of vegetation	*G. submorsitans*		
Density F.B. 100 Y.	♀ %	Gorged %		Density F.B. 100 Y.	♀ %	Gorged %
0·14	52	27	Meadow-pan and woodland savannah	1·37	18	22
0·10	54	40	Along roadside through woodland savannah	1·63	9	42
1·14	44	50	Fringe of residual forest	5·62	7	58
9·27	25	69	Inside residual forest	1·84	15	57

Inside the forest, which forms the true habitat for the species, fly density is very high and 69 per cent. of the old males are gorged, but the female percentage is at its lowest. The percentage of females coming to man decreases as the fly density increases and the tsetse become better fed, suggesting that the females tend to become inactive in the forest in an attempt to avoid the attentions of the huge population of active males (Lamborn, 1915 ; Nash, 1930, 1933a).

G. submorsitans.—In meadow-pan and woodland savannah the density is relatively low, the female percentage is relatively high and the flies are relatively hungry—a combination that is typical of extensive meadow-pan with *G. morsitans* in East Africa. Where a road passes through woodland savannah the density is somewhat higher, the fly are much better fed and the female percentage is much lower ; this state of affairs is typical of a temporary habitat, and not of a feeding-ground. On the fringe of the residual forest, which forms the true habitat for *G. submorsitans*, the density is very high, the female percentage is only 7 and the fly are very well fed. Inside the forest *G. submorsitans* are much scarcer and consequently the female percentage is higher ; but in this case the gorged fly percentage is equally high both inside and outside the forest, so that the higher female percentage does not denote increased hunger but rather that the females avoid the forest fringe because of the male swarms, and appear in greater numbers inside the forest because males are much less numerous.

Summary.

The Seasonal Factor.

1. The period of stress due to extreme climatic conditions is far shorter in the forest than in the meadow-pan.
2. *G. tachinoides* is primarily dependent upon riverine vegetation or residual forest, and has only a very limited wet season spread. *G. submorsitans* is primarily an open woodland fly with great powers of dispersal which are annually checked by adverse climate that enforces a temporary dependence upon the riverine forests.
3. *G. tachinoides* abounds within the stream-bed or residual forest ; *G. submorsitans* abounds on the forest fringe.
4. The dispersal of both species is closely associated with evaporation and saturation deficiency. A mean monthly evaporation of 20–28 cc. and a saturation deficiency of 5 to 8 millibars results in maximal dispersal ; dispersal yields to concentration as the evaporative power of the air increases above these zones.
5. The extent of the annual dispersal is indirectly governed by the duration of the wet season—the longer the season the more extensive the dispersal.
6. The population of *G. submorsitans* steadily increases throughout the rains as the evaporation falls, and becomes maximal towards the end when the evaporation is in the optimum zone (20–25 cc.) ; density steadily falls throughout the dry season as evaporation rises, and becomes minimal at the end when evaporation is maximal. *G. tachinoides* is believed to behave similarly, but the optimum zone of evaporation is probably about 6 to 10 cc.
7. Adult longevity is primarily dependent upon maximum temperature ; it decreases as the temperature rises and increases as it falls. Longevity is greatest in the heavy rains and cold season when the mean monthly maximum temperatures are lowest, being between 85° and 90°F.
8. The frequent occurrence of maximum temperatures between 90° and 100°F. is believed to result in a shortened life, but no immediate fatalities occur until the maximum temperature enters the critical zone (*G. submorsitans* 103·5°–106°F. ; *G. tachinoides* 103°–105°F.).
9. *G. submorsitans* breeds during ten months of the year, and *G. tachinoides* during eleven months. Both species breed freely throughout a tremendous climatic range, the only cessation being in the heavy rains, when an almost saturated atmosphere appears to arrest reproduction.
10. In the early and mid-dry seasons *G. submorsitans* breeds primarily on the floor of small, isolated thickets throughout the open woodland, but in the late dry season it partly evacuates the thickets in favour of the residual forest ; it also uses rot-holes in trees growing in the thickets. *G. tachinoides* breeds extensively in small thickets in the early dry season, then it shifts to the residual forest, and finally, in the hot season, it moves to the moist sand of the river-bed ; it never uses rot-holes in trees.

11. *G. tachinoides* shifts its breeding-grounds as the evaporation rises ; the pregnant females probably evacuate a site when the soil has lost too much moisture. *G. submorsitans* is less sensitive, possibly because its puparia are more resistant to high temperature and low humidity.
12. From the middle of the early rains until breeding ceases in August, *G. submorsitans* breeds under logs in the woodland savannah, whilst *G. tachinoides* breeds under isolated trees on the forest margin.
13. Extensive breeding does not necessarily produce a large adult population ; the seasonal viability of the puparia has a more direct relationship to seasonal fly density than has the breeding rate.
14. The duration of the pupal period is directly related to the mean monthly temperature ; the period varies from an average of 41 days in the cold season, when the mean temperature is about 68°F., to only 18 days in the hot season, when the mean temperature is about 86°F.
15. Fly activity is closely associated with the temperature. Both species are completely inactive when the temperature is below 60°F. or above 105°F. Fly are most active between 81° and 85°F. ; hence in the heavy rains and cold season activity is maximal in the middle of the day, whereas in the hot season activity is then minimal. Tsetse seek to avoid excessive high temperature in the forest by becoming inactive near the ground-level where it is cooler.
16. Excessive evaporation, high maximum temperatures, and a great diurnal temperature range result in a greatly reduced fly population.
17. Locally the following conditions are optimal, but Gadau is near the hot, dry limit of the species' distribution :—*G. submorsitans* : Temperature constant at 79°F. with a saturation deficiency of 7 millibars ; 11 millibars probably results in a higher breeding rate (26°C. and 5 mm., or 8 mm. for breeding). *G. tachinoides* : Temperature constant at 77°F. with a saturation deficiency of 4 millibars ; 11 millibars probably results in increased breeding (25°C. and 3 mm., or 8 mm. for breeding).

An attempt will now be made to co-ordinate the data upon the seasons which are favourable to the different fly functions with the ultimate size of the fly community.

A large tsetse population can only be attained if the climatic conditions of the preceding months favour a progressive increase in the size of each generation. Growth of population must depend directly upon the following factors : (1) Parental longevity, (2) birth rate, (3) pupal period, (4) pupal mortality, (5) climatic conditions when offspring emerge.

Clearly high parental longevity combined with a high birth rate and short pupal period will result in rapid breeding ; but factors 4 and 5 are the key factors, since high pupal mortality or unfavourable climatic conditions for the offspring can frustrate any efforts made to increase the population by factors 1 to 3.

In the heavy rains even though factor 1 is optimal it is ineffectual because factor 2 is then minimal. In the early dry season factors 2, 3 and 4 are probably favourable but are ineffective because factor 5 is unfavourable. In the cold season factors 1 and 2 are almost optimal but are cancelled out by the adverse effects of 3, 4 and 5. In the hot season both key factors (4 and 5) are most adverse. After the break of the early rains factors 2, 3 and 4 are favourable and 1 and 5 are becoming progressively better. By the end of the early rains (2½ months later) breeding has decreased considerably, but this is probably counteracted by all the other factors, which are nearly optimal ; in any case by this time the fly population has increased enormously.

To summarise :—From the heavy rains onwards throughout the dry season insufficient factors are simultaneously favourable—factor is cancelling factor ; but in the early rains the factors essential to reproduction synchronize, and then as the rains progress the climate becomes steadily more favourable for the emerging offspring, culminating with optimum conditions in the heavy rains when density of population is greatest ; but the peak has then been reached, because the wet season cessation of breeding is disastrous to the community, since no new generation emerges until well on into the unfavourable dry season.

It has been shown that the vital functions of the fly are governed by quite different meteorological factors, and that the final result of these fly functions combined, as represented by the ultimate fly density, is related to the evaporation. This is understandable, as evaporation itself is a composite factor, and when evaporation is optimum, favourable medium temperatures and high humidities occur, and when evaporation is excessively high, unfavourable maximum temperatures and very low humidities are recorded ; further there is evidence to show that evaporation directly affects pupal mortality—a key factor. Evaporation epitomizes the individual meteorological factors in the same way that ultimate fly density summarises the final result of the vital fly factors.

The Food Factor.

1. Both species are best fed in the late dry season and early rains when fly and game concentrate near the water. Tsetse are hungry in the heavy rains when floods and long grass cause the river-plain to be evacuated by most of the game ; hunger is greatest in the cold season when low temperature reduces the hours of activity.
2. Seasonal nutrition only depends directly upon climate in localities where the seasonal food supply ceases to be the dominant factor, thus permitting the influence of humidity on the hunger cycle to control the nutrition of the community.
3. Locally, the degree of hunger is never sufficient to affect the community materially ; fly showing signs of starvation are rare.
4. Unlike *G. submorsitans* females, the females of *G. tachinoides* readily attack man ; this species can thrive in isolated colonies surrounded by extensive cultivation, suggesting that it can subsist and reproduce almost entirely on human blood, and hence is a far more serious vector of sleeping sickness than *G. submorsitans*, which is only found in thinly populated areas where game animals still survive.
5. Females of both species attack man most readily in the seasons when game is scarcest.
6. *G. tachinoides* is always better fed than *G. submorsitans*, probably because of its ability to thrive on either mammalian or reptilian blood ; also, its sedentary habits keep it in the vicinity of the forest islands where game and reptiles are never entirely absent.

The food factor is considered to be the least important of the three great factors that govern the existence of tsetse ; locally, food shortage has never been sufficiently pronounced to affect the community adversely. As in Tanganyika, fly density is highest when game is scarcest and lowest when game is most abundant ; climate is the vital factor, not food, which always suffices.

The Vegetation Factor.

1. The residual forest islands provide the true habitat for both species ; they offer the fly protection when the climatic conditions elsewhere are insupportable, and provide suitable breeding-grounds and an adequate food supply ; further they are resistant to fire and flood.
2. The woodland savannah with its small thickets is the temporary habitat of *G. submorsitans*, and for many months in the year enables this species to spread and maintain itself at a considerable distance from the residual forest. To a much lesser extent this is true for *G. tachinoides*.

3. It is suggested that the term " meadow-pan " might be employed in the tsetse literature to replace the confusing collection of local native names that are at present used in describing this type of seasonal swamp.
4. Both species are most numerous and are best fed in the vicinity of the residual forest or true habitat. *G. submorsitans* lives mainly on the forest fringe, but *G. tachinoides* lives within.
5. Pronounced female centres and feeding-grounds of the East African type do not occur ; however, catches from the open country do show a higher female percentage and greater hunger. The higher the fly density the lower the female percentage.

From an economic aspect there can be no doubt that vegetation is by far the most important factor ; we cannot alter the Nigerian climate, but by modification of the vegetation which forms the true habitat we may be able to modify the forest's microclimates until they become incapable of befriending the tsetse in its time of need.

General Conclusions and their Practical Application in Nigeria.

The mechanism required to produce a large tsetse community is greatly hindered by a climate that is usually adverse. The machinery is constantly being thrown out of gear by a meteorological factor committing an act of sabotage to a vital part of the mechanism ; admittedly the machine keeps running, but inefficiently for months at a time. Once a year, however, there is a cessation of sabotage and the machine really functions as a whole and becomes so productive that it makes up for previous losses ; and so the tsetse community goes struggling on, but never a really thriving concern like its East African relatives which have managed to extend and consolidate themselves over a great part of the country.

G. submorsitans has probably reached the limit of its distribution in northern Nigeria. There is no chance of its colonising great tracts of woodland ; it has attempted it every rains, probably for centuries, but the severity of the dry season has annually thrown it back with heavy losses to the vicinity of the rivers ; in wetter years it is more successful, but it cannot retain its gains.

This limited distribution of *Glossina* in northern Nigeria is advantageous in that there are large, fly-free areas where cattle can be grazed ; but since both man and *Glossina* concentrate near permanent water there is a far greater incidence of sleeping sickness than would occur if the fly were uniformly distributed over enormous tracts of country ; it is this closeness of man-fly contact, resulting in a relatively large percentage of infected tsetse, which causes such a high incidence of the disease.

It has been shown that *G. submorsitans* has far greater powers of dispersal than *G. tachinoides*, and that both the adults and puparia are better equipped to withstand adverse climatic conditions, rendering the species far less reliant upon the true habitat ; however, *G. submorsitans* is dependent upon game, which confines its distribution to the less populated areas where it can do less damage. The result is that this species is far harder to exterminate but is also of less economic importance, so that no efforts should be made to attempt its destruction whilst there are so many easier and more important problems in which only *G. tachinoides* is involved.

The comparative study of meteorological conditions in the open country and forest showed that retarded desiccation in the true habitat resulted in a greatly decreased period of stress for its tsetse community, but that by the end of the dry season the climatic differences between the untenable open country and the tenable forest was no longer great, suggesting that even in the sanctuary the fly survive by only a narrow margin.

By clearing the peripheral and intrusive thickets the dry harmattan wind would be enabled to penetrate the forest islands, and it might so accelerate and accentuate the desiccation of the forest floor that a very high pupal mortality might be induced in the cold season ; further, by premature desiccation the soil evaporation in the late dry season might be reduced sufficiently to prevent the occurrence of specially low temperatures at ground level, which just enable the fly to survive under normal conditions.

Now that the general ecological investigation has been completed, a field experiment in partial clearing is to be carried out. If the research findings are confirmed, and it is found that *G. tachinoides* can be driven out of the true habitat by only a slight modification of the vegetation, there may be a big future for partial clearing in the hotter and drier parts of West Africa. Instead of cutting down all the vegetation along the whole length of a stream, it may be possible to exterminate the fly by the removal of undergrowth only, the large trees being spared—a great saving in clearing costs and in timber.

A still further refinement may be possible. When surveying typical *G. tachinoides* streams in the late dry season, the writer has observed that one can walk for long distances in the stream-bed under the dense shade of the riverine vegetation and never meet a single tsetse ; then one comes to a pool, puddle or patch of wet sand, and immediately a few fly will be caught. In view of the research results, it seems probable that the fly have evacuated the intervening areas, and have concentrated at these spots where reduced temperature and higher humidity enable them to survive and also to breed. It is possible that by clearing the vegetation only around these vital spots fly could be driven out of many miles of the upper reaches of these streams ; further down their courses, where they join the big rivers and permanently hold water, barrier clearings would have to be constructed to prevent the fly from penetrating the upper reaches during the rains. Apart from a great saving in cost, such a plan would remove the necessity of cutting down riverine vegetation on the higher ground where erosion might take place.

PART II.

An Ecological Comparison of the East and West African Races of *G. morsitans*.

The writer has had opportunities of studying the two races of *G. morsitans* on each side of Africa over a period of nine years ; the two investigations have been carried out in two such very different climates that it is interesting to compare the reactions of the two races to their entirely different environments.

1. Comparison of the Two Climates, with suggestions as to the Climatic Limits for the Species.

The climate on both sides of Africa was investigated with similar meteorological instruments, kept in similar Stevenson screens at a similar height (4 feet) ; since similar localities in typical open *morsitans* country were chosen, the summarised data in Columns I and II of Table XX are strictly comparable. Annual means are shown, but the highest and lowest monthly means ever recorded are also given in brackets, so as to indicate the possible range.

It will be noted that the mean annual saturation deficiency and evaporation are about twice as great in the West African Station, but that the rainfall is only six inches less ; this is primarily due to a much poorer distribution of rainfall in northern Nigeria, where the dry season is two months longer and the rains two months shorter than in central Tanganyika. This reduction in the ratio of wet to dry months limits both the density and the distribution of the species in West Africa.

TABLE XX.

A Comparison of the Mean Annual Meteorological Data from G. morsitans *Fly-belts at Kikori in Central Tanganyika, and at Gadau in Northern Nigeria.*

Meteorological factors	East Africa (Kikori)	West Africa (Gadau)		Period of observations in months	
	Col. I Station in open *morsitans* bush	Col. II Station in open *morsitans* bush	Col. III Station in residual forest	Kikori	Gadau
Rainfall (inches)	38·8 (0–13)	32·8 (0–20)		48	72
Sat. deficiency (millibars) ...	6·6 (3–14)	15·7 (5–29)	12·1 (2–26)	23	29
Evaporation (cubic cms.) ...	31·0 (7–65) (In sun)	59·0 (12–122) (In sun)	26·0 (3–55) (In shade)	39	36
Maximum temp. (°F.) ...	80·8 (73–89)	93·9 (85–104)	87·7 (80–99)	39	29
Minimum temp. (°F.) ...	60·0 (51–65)	61·1 (51–77)	66·9 (54–77)	39	29
Mean temp. (°F.)	69·2 (62–75)	78·8 (68–88)	76·4 (67–87)	39	29

N.B.—The figures in brackets indicate the possible monthly range, being the extreme mean monthly figures ever obtained.

Turning again to Columns I and II it will be seen that Gadau is far hotter, with an annual maximum temperature that averages about 13°F. higher, and with the possibility of a mean monthly maximum of 104°F. as against a possible 89°F. at Kikori. Minimum temperatures are not so strikingly different.

We may conclude that the climate in the *morsitans* bush at Gadau is much hotter and twice as dry as that experienced by tsetse at Kikori in Tanganyika.

Kikori, in East Africa, has an elevation of 4,158 feet above sea-level, and lies at the foot of an escarpment that rises in places to almost 6,000 feet ; *G. morsitans* is very scarce above 5,000 feet. The early dry season is characterised by mornings with drizzling rain from the clouds that hang over the escarpment, and it is generally considered that the climate of this fly-belt represents an approach to the cold, wet end of the range of the species in East Africa ; the belief was strengthened when the torrential rains of 1930 almost exterminated the tsetse community.

Gadau in West Africa has an elevation of only 1,200 feet and lies in the flat Lake Chad basin ; it is not very far from the southern edge of the Sahara desert, and no *G. submorsitans* have ever been found more than 60 miles further north ; hence the Gadau climate can be taken as representative of the hot, dry end of the range of the species.

A comparison of the Gadau and Kikori climates should give a general idea of the upper and lower climatic limits which control the range of this species in Africa.

It would be unfair to take the data from the Gadau Meadow-pan Station as representing the upper limit, because its climate must be above this limit in the late dry season when such country is annually evacuated by the fly. For this reason the data for the Forest Station are given in Column III, as we do know that this species can just survive in the forest climate. When referring to the lowest monthly means in the brackets in Column III, it should be remembered that the forest is evacuated in the heavy rains in favour of more open country, so that at that time the lowest monthly means given in Column II are more applicable ; hence it would be fairer to say that the species exists through a mean monthly saturation deficiency range varying from 5 to 26 millibars, and an evaporation range of 12 to 55 cc. (N.B.—Evaporation figures in Columns I and II are strictly comparable, the atmometers having both been exposed in open sunlight, but the forest evaporation, Column III, has been greatly influenced by the heavy shade canopy ; the saturation deficiency readings, in common with all the other data, were obtained from instruments housed in Stevenson screens and hence kept under similar shade conditions.)

Since the difference between the readings of Columns II and III is relatively not very great, should we take the mean between the two sets of figures so as to allow for the seasonal changes in the environment of *G. submorsitans*, we are certain to get a set of yearly means that must be very near the upper limit for the species ; in conjunction with the Tanganyika figures we shall then have the approximate upper and lower climatic limits in between which this species can range. Such figures are given below, Kikori supplying the lower and Gadau the upper limit for each meteorological factor ; the figures refer to annual means only :—

Saturation deficiency	6–14 mb.	(4·5–10·5 mm.)
Evaporation	31–42 cc.	
Maximum temperature	81°–91°F.	(27·2–32·8°C.)
Minimum temperature	60°–67°F.	(15·6°–19·4°C.)
Mean temperature	69°–78°F.	(20·6°–25·6°C.)

No range for the mean annual rainfall is given, because it is not the total precipitation but the distribution which affects tsetse.

It is suggested that there will be no *G. morsitans* belts in those parts of Africa where the annual means for the meterological factors quoted are all appreciably outside the ranges given. It must be realised that the figures shown above are only a pioneer attempt to give some idea of the approximate climatic limits which restrict the geographical distribution of this species : a rough idea should be better than none.

2. The Laws governing the Seasonal Density of G. morsitans.

It was explained on p. 115 that ultimate fly density summarises the effects of the various fly functions combined, and that, similarly, saturation deficiency and evaporation summarise the effects of the various meteorological factors ; further, it has been shown that seasonal fly density in both East and West Africa is closely related to the saturation deficiency and evaporation of the same and previous months. If we can now show that the same degrees of saturation deficiency and evaporation are associated with optimum conditions and maximal fly density on both sides of Africa, we shall then have gone a long way towards proving that (*a*) the size of the fly community is governed by definite fixed meteorological conditions, and not by the abundance of buffalos, or some other fantastic idea ; (*b*) physiologically the two races of *G. morsitans* are probably very similar.

TABLE XXI.

Relationship between Saturation Deficiency and the Size of the Fly Population.

Mean monthly saturation deficiency (millibars)	Kikori, Tanganyika		Gadau, N. Nigeria	
	No. of months	Mean fly density	Mean fly density	No. of months
0–2	0	—		0
3–4	9	497		0
5–6	4	543	222	2
7–8	5	298	193	3
9–10	1	182	—	0
11–15	3	168	73	8
16–20	0	—	64	8
21–25	0	—	38	3
26–30	0	—	30	4
	22			28

In Table XXI all the mean monthly saturation deficiency and fly density data collected at Kikori and Gadau have been condensed as follows : The saturation deficiency data have been grouped into zones of 2 millibars each, between 0 and 10 mb. and into 5 millibar zones between 11 and 30 mb. ; against each zone is placed the mean fly density figure, which is the average of all those catches made in the months when the saturation deficiency was within that zone. The saturation deficiency for both the same and previous months shows a good relationship with the fly density, but only data for the same month are given in the table in order to save space, and also because the relationship is certainly better.

Looking at the figures for Kikori, Tanganyika, it will be seen firstly, that very high fly density occurred in the 9 months when the mean saturation deficiency was between 3 and 4 millibars ; secondly, that maximum density occurs in the 5–6 millibar zone ; and thirdly, that as the saturation deficiency rises above 6 millibars so the fly density falls. Turning now to the figures for Gadau, N. Nigeria, it is clear that a mean monthly saturation deficiency of 5 to 6 millibars also affords optimum conditions, and that as the saturation deficiency rises above this optimum so does the fly density fall.

Such an amazing agreement in data collected under such vastly different climatic and geographical conditions tempts the writer to suggest the following law :—

> *The population of* G. morsitans *in both East and West Africa will be greatest when the mean monthly saturation deficiency lies between* 5 *and* 6 *millibars* ; *as the saturation deficiency rises above this optimum zone, so the population will decrease.*

It is probable that the density also diminishes if the saturation deficiency falls below this zone, but data for that end of the range are unobtainable in Northern Nigeria.

Returning again to Table XXI, it will be seen that between 3 and 8 millibars high fly densities can occur, and that whereas the mean monthly saturation deficiency was in that zone for 18 out of 22 months at Kikori, it was only in that zone for 5 out of 28 months at Gadau. This is a most instructive point. Unfortunately for the West African race it appears to be physiologically the same as the East African form, and hence its activities are regulated by the same meteorological laws ; had its optimum zone been higher it would have had many more months of favourable conditions, resulting in greater density and wider dispersal. Like the European in the tropics, it has managed to adapt its habits to the local environment, but not its constitution.

The writer has already published extensive results showing that at Kikori maximum fly density occurs when the mean monthly evaporation is between 20–25 cc., and that as the evaporation rises above or falls below this zone, so does fly density decrease (Nash, 1931, 1933a, 1933b).

TABLE XXII.

	Gadau, N. Nigeria	
Mean monthly evaporation (cc.)	No. of months	Mean fly density
Under 20	2	140
20–24	3	240
25–29	1	204
30–59	9	143
60–89	13	55
90–119	4	32
120–159	1	15
	33	

It will be seen from Table XXII, which is similar in principle to the previous table, that the West African race behaves in like manner, and has the same optimum zone. Note again how few are the favourable months. The lag between a change in the evaporation and its effect upon the population is far shorter in West Africa, the relationship being much better if the evaporation of the same month is taken.

It might be excusable to suggest the following law :—

> *The population of* G. morsitans *in both East and West Africa will be greatest shortly after or whilst the mean monthly evaporation lies between* 20 *and* 25 *cc., as measured by a Livingston white atmometer sphere. As the evaporation rises above or falls below this zone, so the population decreases.*

The two races have identical optimum zones for saturation deficiency and evaporation, but as will be seen from Table XXIII their optimum temperature zones are very different.

TABLE XXIII.

Mean Monthly Temperature and Mean Fly Density grouped.

Mean monthly temperature	Kikori, Tanganyika		Gadau, N. Nigeria	
	No. of months	Mean fly density	Mean fly density	No. of months
62–64°F.	6	390		0
65–67 ,,	8	677		0
68–70 ,,	10	487	32	3
71–73 ,,	11	424	47	5
74–76 ,,	3	266	42	2
77–79 ,,	0		155	3
80–82 ,,	0		145	8
83–85 ,,	0		44	5
86–88 ,,	0		34	3
	38			29

Maximal fly density corresponded with mean monthly temperatures of 65–67°F. at Kikori, but 77°–82°F. at Gadau. This tremendous difference confirms the writer in his opinion that the density of the population of *G. morsitans* is related to the evaporative capacity of the air, and suggests the following law :—

> *Providing the mean saturation deficiency and evaporation are optimal, the population of a* G. morsitans *fly-belt will be maximal, irrespective of the mean temperature (within wide limits).*

Kikori is considered to represent the cold, wet limit of the range of *G. morsitans*, and Gadau the hot, dry limit, hence it is obviously unwise to take the local optimum conditions from either place alone as representative of the most favourable conditions for the species. Since, however, the optimum zones for saturation deficiency and evaporation are identical, even at the opposite extremes of the range of the species, these figures may be taken as correct ; but the temperature zones are very different, so that a mean between these two extreme sets of locally favourable figures should give an approximate idea of the true optimum temperature for the species. Such a mean has been taken, and the following meteorological conditions are suggested to the laboratory worker as affording the most favourable conditions for keeping *G. morsitans* :—Saturation deficiency constant at 6 millibars (4·5 mm.) ; temperature constant at 73°F. (22·8°C.). By raising the saturation deficiency breeding will be increased, but possibly at the expense of the community.

3. The Summarised Ecology of the East and West African Races of G. morsitans.

1. The small residual forest islands of N. Nigeria are analogous to the extensive *Berlinia-Brachystegia* woodlands of Tanganyika, in that both form the true habitat of *G. morsitans.*
2. In both countries extensive meadow-pan provides a thinly populated feeding-ground with a high female percentage, tsetse being hungrier there than elsewhere ; but in West Africa, dry season concentrations of hungry tsetse showing a high female percentage never form within small meadow-pans, such sites being uninhabitable at that season.
3. Females of both races attack man most readily where fly density is lowest, and least readily where the density of population is greatest.
4. The percentage of females emerging from thousands of puparia collected in the bush was 50 per cent. at Kikori and 51 per cent. at Gadau, but the average female percentage among fly that attacked man was only 11 per cent. in each fly-belt, suggesting that the females of neither race is partial to human blood.
5. Seasonal nutrition at Gadau is directly controlled by seasonal food-supply, and not by seasonal humidity as in Tanganyika. Since the influence of humidity upon hunger can be cancelled by pronounced seasonal fluctuations in the local food supply, the seasonal nutrition cycle is bound to vary throughout Africa.
6. At both Kikori and Gadau *G. morsitans* is scarcest when game is most abundant, indicating that the climatic factor controls fly density, not the food factor.
7. Both races are inactive in the early mornings of the cold season ; in view of results from extensive work in Nigeria, this inactivity is probably due to low temperature. The excessive heat of the West African late dry season causes pronounced mid-day inactivity, which was never observed in Tanganyika. Both races are normally inactive shortly after sunset.
8. Both races tend to attack man above knee height, unlike *G. tachinoides* which attacks the ankles.
9. As the evaporation rises throughout the dry season both races concentrate in their true habitats, but concentration is far more pronounced in N. Nigeria owing to the severer climate and the much smaller areas covered by the true habitat.
10. Both races disperse when the rains break and the evaporation falls, but the longer wet season in Tanganyika results in much more extensive dispersal, and the milder dry season that follows enables these advances to be consolidated, new fly-belts thus being formed. All attempts made at colonisation during the rains are annually checked in Nigeria by the severity of the following dry season.
11. In East Africa *G. morsitans* breeds primarily under fallen trees, but in West Africa it breeds promiscuously on the floor of thickets and forest islands—an adaptation to the climate, as shown by its reversion to logs in the few favourable weeks at the end of the early rains. Both races sometimes use rot-holes in trees, but such sites are only used in N. Nigeria if the trees grow within thickets.
12. Owing to the difference in breeding habits, log traps of the type that were very attractive to the East Africa race, are unattractive in N. Nigeria.
13. With the exception of the heavy rains, when breeding partly or completely stops, both races reproduce throughout the year. Breeding is maximal in the early rains, but is also considerable in the first half of the dry season, especially in East Africa.

14. *G. morsitans* can breed through a great range of climatic conditions ; only very high humidity and low evaporation seem to affect reproduction.
15. In both races the duration of the pupal period depends upon the mean monthly temperature, being shortest in the hot months and longest in the cold. The variation at Kikori was 29–52 days, and at Gadau 19–41 days.
16. The density of the population of both races follows a seasonal cycle that is basically the same ; density decreases in the dry season, becoming minimal towards the end ; density starts to increase at the beginning of the rains, becoming maximal some months later (fig. 5, p. 98). This density cycle is closely related to the seasonal saturation deficiency and evaporation.
17. When the mean monthly saturation deficiency is between 5 and 6 millibars and the mean evaporation is 20–25 cc., the population of both races is maximal ; as the saturation deficiency and evaporation increase above or decrease below these optimum zones, so does the fly density decrease.
18. Providing that the mean saturation deficiency and evaporation are optimal, the population in a *G. morsitans* fly-belt will be maximal, irrespective of the mean temperature (within wide limits).
19. Since identical conditions of saturation deficiency and evaporation are associated with optimal conditions for both races, it is suggested that they are physiologically similar, and that their vital functions are governed by identical laws. This would account for the different nature of the true habitat selected by the West African race, which, having failed to adapt its constitution to the climate, has perforce adapted its habits ; had it evolved a constitution which preferred a higher degree of evaporation and temperature, the greater frequency of optimum conditions would have enabled it to become as widespread a pest as its East African representative.
20. It is considered that optimum conditions for *G. morsitans* could be reproduced artificially by keeping the saturation deficiency at 6 millibars (4·5 mm.) with the temperature constant at 73°F. (22·8°C.), by raising the saturation deficiency breeding would be increased, possibly at the expense of the community.

4. Conclusions.

A reviewer of the tsetse literature would, I think, conclude that many of the authors had become imbued with the idea that tsetse behave in different ways in different fly-belts, and that a disparity in results is only to be expected. Logically, one should start an investigation into the ecology of a species by assuming that there will be a great physiological resemblance between the individuals, resulting in the existence of a series of natural laws which control the species from one end of its range to the other.

In order to discover the laws which govern the vital fly functions, and the fundamental law which controls the density of the population, one first needs several identical eco-climatic field investigations, carried out at the opposite climatic extremes of the range of the species ; a laboratory investigation should then follow, designed to amplify and standardise the laws suggested by the field results. Until all the basic laws have been discovered the edifice of tsetse literature will continue to have no foundations.

Undoubtedly some of the conclusions in this paper need to be refined by laboratory methods, but it is hoped that they will stimulate tsetse workers to a much wider view of the problem, and to the realisation that *G. morsitans* is probably governed by the same basic meteorological laws throughout the whole of its African range. The differences in behaviour observed in various fly-belts do not denote fundamental physiological differences in the communities, but rather mere superficial adaptations of habit to the local environment. Since much of the past work has been a study of habit, it is not surprising that results differed from place to place.

Acknowledgments.

I am grateful to Dr. H. M. O. Lester, who is in charge of the Sleeping Sickness Service, for his kindness in always arranging practical help whenever required, and to Mr. A. G. F. Jones, Technical Assistant, for having kept an eye on the work in my absence. Acknowledgments are also due to Capt. A. S. Thornewill (Forestry Dept.) for valuable information upon the vegetation communities of this district.

The method employed in studying the climate was based on the technique used by Prof. J. F. V. Phillips in Tanganyika ; I owe much to him for his instruction in this branch of ecology.

I am greatly indebted to Prof. P. A. Buxton for his stimulating criticism, and constant advice, and also to Mr. C. F. M. Swynnerton, my late Director in Tanganyika, for the encouragement he gave me when I worked in East Africa.

I cannot pay too high a tribute to my Hausa assistants, Mallams Ibrahim, Dau, and Lawal ; they have combined trustworthiness with intelligence and physical endurance—a rare combination. They have cheerfully faced hours of wading out to the instruments in the rains, and the misery of all day catches in the terrific heat of the dry season. Without such assistants the work described could never have been done.

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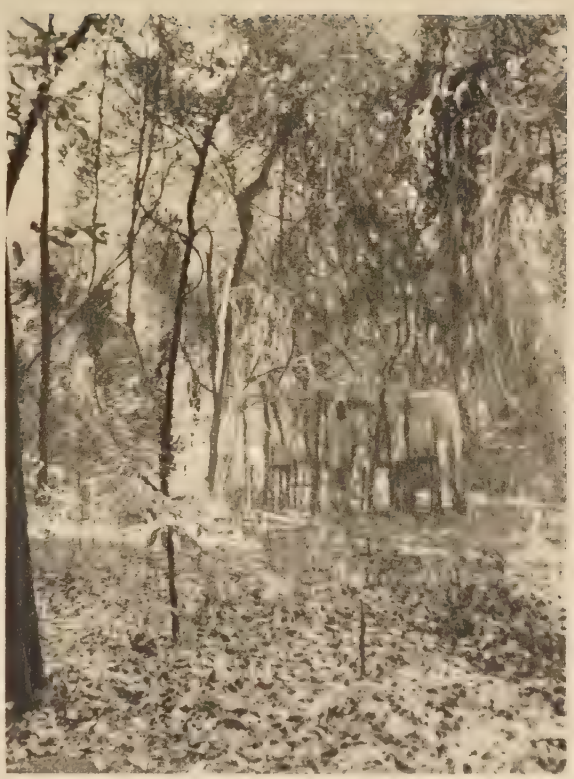

Fig. 1. The Residual Forest Instrument Station.

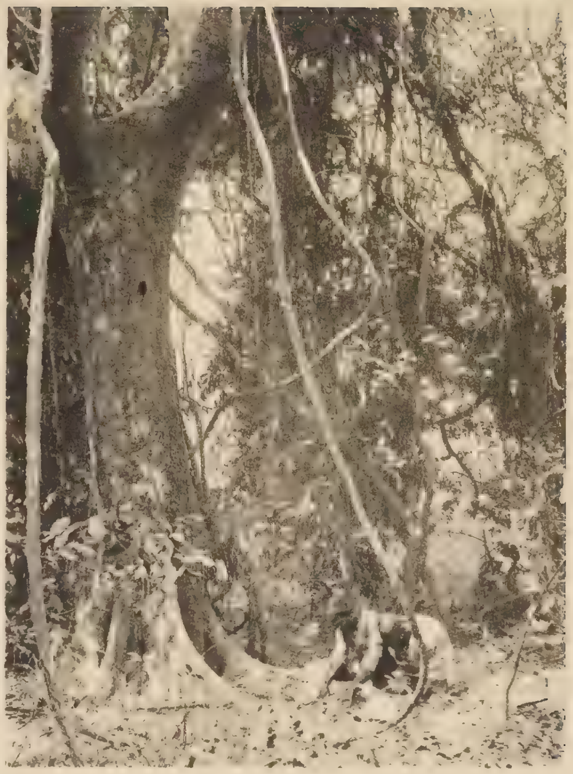

Photo. by P.A. Buxton

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Fig. 2. Searching in Forest for *G. tachinoides* Puparia.

WITHIN A RESIDUAL FOREST ISLAND
(THE TRUE HABITAT).

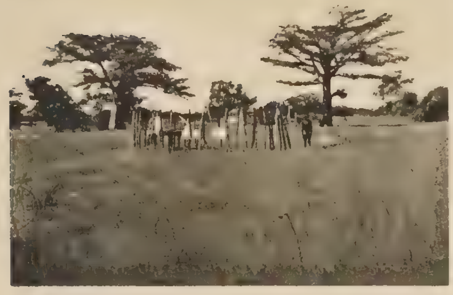

Fig. 1. Meadow-Pan as "meadow." (Rains).

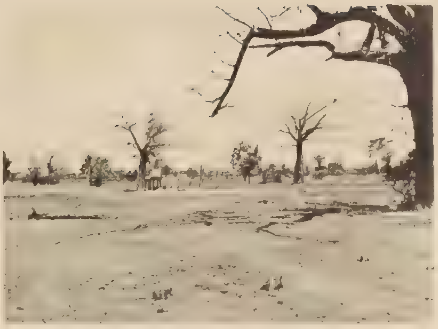

Fig. 2 Meadow-Pan as "pan." (Dry Season).

THE MEADOW-PAN INSTRUMENT STATION.

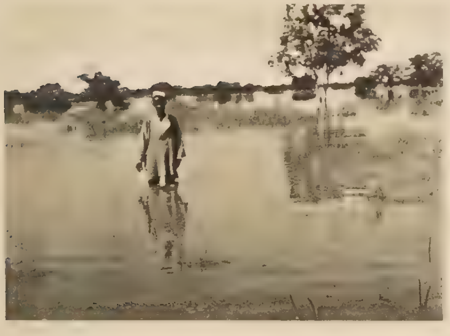

Fig. 3. The Meadow-Pan is Inundated.

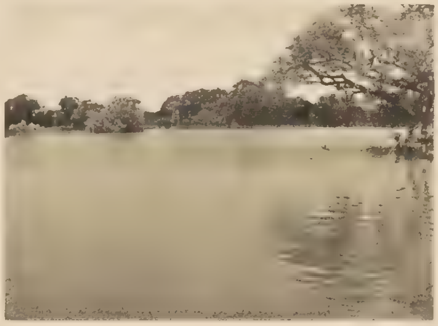

Fig. 4 The True Habitat is raised above flood level.

THE SEASONAL FLOODS (HEAVY RAINS).

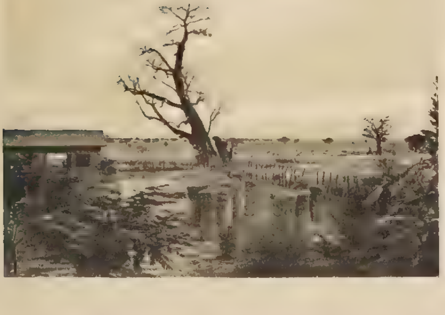

Fig. 5. Without Harmattan.

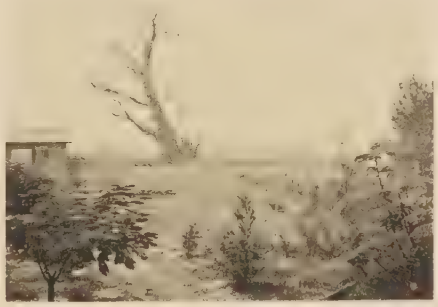

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Fig. 6. With Harmattan.

THE HARMATTAN DUST HAZE.

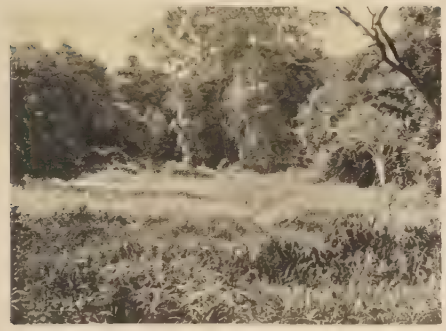

Fig 1. Residual Forest Island in Rains. (True Habitat).

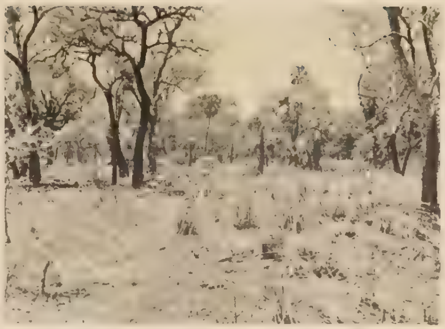

Fig. 2. Heavy Woodland Savannah, after usual patchy burn. (Temporary Habitat).

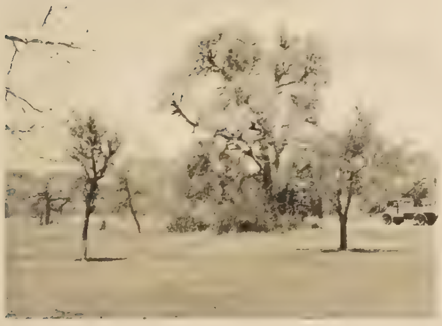

Fig. 3 Small Isolated Thicket after Fires.

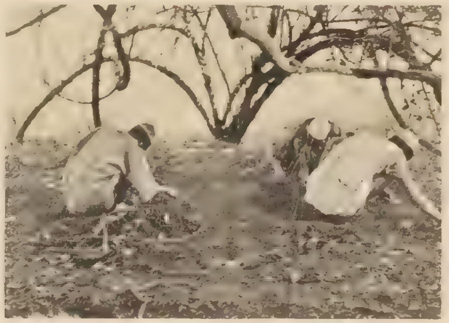

Fig. 4. Searching for *G. submorsitans* Puparia in Isolated Thicket.

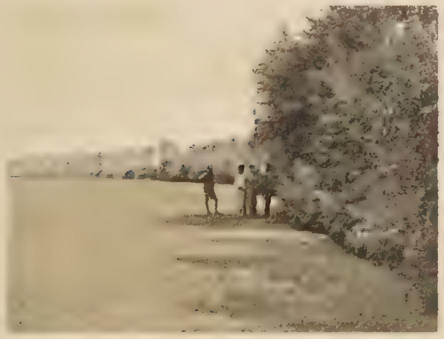

Fig. 5. Margin of Sandy River-Bed. A Breeding Ground of *G. tachinoides.*

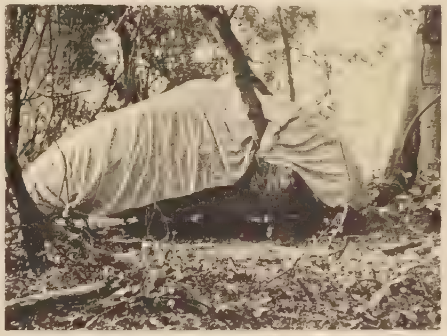

Fig. 6. The Puparia Hut on Edge of Forest.

THE DISTRIBUTION OF TSETSE-FLIES IN TANGANYIKA TERRITORY.

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(Map.)

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1. Introduction.

Tanganyika Territory, sandwiched between Kenya and Portuguese East Africa and lying between latitudes 1° and 12° South and longitudes 30° and 40° East, is an East African territory of some 366,000 square miles, of which at least two-thirds (the Veterinary Department estimates it at three-quarters) are infested with tsetse-flies. Their distribution has never been described in detail, and the published information available is scanty in the extreme. For this reason the following account is offered, attempting no more than to place on record the present state of our knowledge of the subject, which is recognised to be far from complete ; there is no doubt but that future surveys, particularly in the southern areas of the Territory, will furnish more details, especially of the distribution of the rarer and more localised species. It is, however, claimed that the outlines of the fly-belts as depicted on the map do represent the general distribution of fly in the Territory to-day, and that such changes as are found in future years will represent invasions or withdrawal of the fly.

2. Acknowledgments.

I am especially indebted to Mr. C. F. M. Swynnerton, Director of Tsetse Research, Tanganyika Territory, for placing at my disposal his unique and very extensive knowledge of the fly-belts of this Territory, and in particular for the use of his map of the distribution of fly which combined the results of his initial reconnaissances of the country during 1921–22, with the information received from circularising various Government officials, and subsequent observations from time to time. This, added to and revised in the light of my own investigations since 1925 (confined to the country lying north of the Central Railway) and of the various sources acknowledged below, forms the basis of the present account.

I am further indebted to all my colleagues of this Department for the free use of their observations on the distribution of the fly in the various parts of the Territory in which they have worked, and in particular to Mr. B. D. Burtt, whose extensive travels in the Eastern, Central and Northern Provinces of the Territory have provided so much valuable information.

I wish also to place on record my appreciation of the co-operation of the Veterinary Department, which has taken the form of the collection of specimens of tsetse by members of the Department during their travels, and the provision of such information as they have obtained on this subject ; to all these I tender my thanks. It is a particular pleasure to acknowledge the help of the present Director of Veterinary Services, Mr. Hornby, not only along these lines, but also in placing at my disposal his map outlining the distribution of the cattle areas of the Territory in 1933 (unfortunately never published), which has assisted the filling in of the general outlines of the fly-belts, particularly in the southern areas for which our knowledge of the precise limits of the fly is incomplete.

I am also glad of the opportunity to thank Dr. Maclean, Deputy Director of Medical Services (until lately Sleeping Sickness Officer for the Territory), for the ready way in which he has always given me the benefit of his knowledge of fly distribution, and to thank as well all those of his assistants who have sent me information and specimens.

To Mr. Gillman's recently published Population Map of the Territory I owe certain corrections to the extent of the closely settled, fly-free country in the Pangani and Rufiji River areas.

For reading through the manuscript, constructive criticism and helpful suggestions, I am indebted to Messrs C. F. M. Swynnerton, N. H. Vicars, C. H. N. Jackson, B. D. Burtt and S. Napier-Bax.

3. Existing Information.

Old records of the distribution of tsetse in Tanganyika are scanty, and in fact no comprehensive account giving details of the different species exists. A map was published in "Die Deutschen Schutzgebiete in Africa und der Südsee," 1912–13, showing various belts of fly, but this cannot be regarded as giving all the information available even at that time, for no tsetse-belt is shown in the Kondoa area, although Obst during his travels in 1911-12 had found tsetse numerous at Kikori in that area (Jackson, 1933, p. 212). Morstatt (1913) included the tsetses of the Territory in a general list of its blood-sucking flies and ticks. Speiser (1924) gives 5 species of tsetse-fly as occurring in the Territory, but gives no details of their distribution therein ; incidentally, his inclusion of *G. tachinoides* in this list must be regarded as referring to *G. austeni*, a mistake which has been made elsewhere. Wölfel (1916) describes the distribution of tsetse in Tanganyika Territory with a map, which has formed the basis of a subsequent one, embodying observations between 1916 and 1921, published in the Annual Report of the Director of Veterinary Science and Animal Husbandry for 1923 ; this map was again revised and brought up to date in the report of that Department for 1927. These maps do not distinguish the different species of tsetse, merely giving the general outline of the fly-infested areas.

The published records up to 1923–24 were summarised by Newstead (1924), and these were incorporated in his maps, which are again on too small a scale to do justice to the detailed distribution of the different species of fly within a single territory. Since then various relevant references are to be found in the literature, mainly incidental to other matters ; these notably occur in the publications of members of this Department (and particularly Swynnerton, 1923 a and b), and in the Annual Reports of the Veterinary and Medical Services of the Territory. Specific references will be made below in the detailed accounts of the species mainly to Newstead (1924) and to subsequent publications.

There still remain three papers which must be mentioned here. The first (Frantzen, 1924) gives a general summary of the geographical distribution of tsetse-flies, with a map again too small to give really precise information. The remaining two (Zumpt, 1935 a and b) embody some observations on the distribution (and systematics) of *G. palpalis*, and a most useful collection of the records of species of tsetse from the German Museums ; to these papers I shall refer again later.

4. The Species of Tsetse concerned.

Eight different species of tsetse are to be found in Tanganyika Territory ; they are—*Glossina brevipalpis*, Newst., *G. longipennis*, Corti, *G. fuscipleuris*, Aust., *G. palpalis*, Rob-Desv., *G. morsitans*, Westw., *G. swynnertoni*, Aust., *G. pallidipes*, Aust., and *G. austeni*, Newst. *G. tachinoides*, *G. fusca* and *G. tabaniformis*, have been recorded from the Territory, but these were undoubtedly mis-identifications, the first for *G. austeni* and the other two for *G. brevipalpis*. It is not very likely that any addition will be made to this list in the future, at least from the species of tsetse now known, unless by the finding of *G. fusca* var. *congolensis* along the western borders of the Territory ; it is, however, probable that the Central Rift Valley which forms these borders is a natural barrier to its eastward spread.

G. brevipalpis, Newstead.

This species is spread widely over the Territory, but is restricted to small local occurrences. Its chief areas are to be found in the Musoma District (in the fringing forests of the shores of Lake Victoria, and of the rivers and streams running into the lake), in the Arusha-Moshi area (on the heavily forested rivers and streams which run down from those great ancient volcanoes, Meru and Kilimanjaro), and on the forested slopes of the Usambara Mountains and of the Kaguru and Uluguru Ranges. The widely separated records from the southern part of the great eastern fly-belt suggest that were more detailed surveys carried out there it would be found to occur much more frequently.

An interesting record has lately come from the Island of Mafia, where Mr. W. V. Harris, Assistant Entomologist to the Agricultural Department, found three specimens in March 1933 ; more examples were found in December of that year by the Veterinary Department. There is a suggestion, however, that the infestation of the island, confined to one small area, is not a permanent one, but that the flies are merely carried across from time to time by dhows from the mainland. Other centres which must be mentioned are those of Dar-es-Salaam and its vicinity, and the Kigoma area. Finally, a small belt of fly is marked on the Veterinary Map (1933) at the north end of Lake Nyasa ; this I ascribe to *G. brevipalpis* on the strength of a record by Mr. C. Smee, Entomologist to the Agricultural Department of Nyasaland, in October 1926 ; Zumpt (1935 b) may be referring to this belt when he records the species from Lake Nyasa.*

The localised occurrences of *G. brevipalpis* are due to its requirement of heavy thicket affording dense shade (Swynnerton, 1936, and others) ; its confinement to such situations prevents it from ranging freely through a country which consists so largely of open savannah woodland. Its widely interrupted range is doubtless the relic of a much more universal distribution during the pluvial periods which characterised East Africa generally at the time of the Pleistocene Glacial Ages of Europe (Wayland, 1930, Leakey, 1931, Chapter II, and Brooks, 1931) ; these must have allowed a much heavier and moister type of vegetation to be widely distributed (Moreau, 1933). Our records are probably still more scanty than they should be, as this species, shunning the bright light of the open savannahs, lurks during the day in the recesses of its thicket homes, probably doing most of its food-hunting in the dusk or even at night, and so not ordinarily coming into contact with the casual traveller, and requiring special search.

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* The correct conditions for *G. brevipalpis* abound in the great Eastern Tsetse Belt of Tanganyika, and I have found it there wherever I have looked for it. This is undoubtedly its main area in Tanganyika. The Mwaya fly-belt to the north of Lake Nyasa contains *G. brevipalpis*, which occurs in Nyasaland also.—C. F. M. Swynnerton.

Glossina longipennis, Corti.

This species spreads into Tanganyika Territory from more extensive belts in Kenya in two places—south and east of Moshi, and again in the Lake Natron region ; I have shown, after Lewis (1935), the record in Kenya nearest to the last region. *G. longipennis* seems well distributed in the south-eastern corner of Kenya, and the occurrences near Moshi are an extension of this belt.

Whilst the general consensus of opinion is that this little known species is a lover of the semi-desert areas, my own sole experience of it coincides with that of Mr. T. J. Anderson (Lewis 1934 ; also Newstead, 1924, p. 101) ; in fact, not only did I find it inhabiting moist country typical of *G. brevipalpis*, but I also actually took the two species together. Three specimens in all were caught, all in the neighbourhood of Arusha Chini, some 20 miles south of Moshi, near the junction of the permanently flowing Kikuletwa River with streams from Kilimanjaro and the Ruvu River from the North Pares to form the great Pangani River. The first, a male, was taken with twenty males and one female of *G. brevipalpis* along a series of paths through heavy riverine fringing forest ; it was noticeable that the *longipennis*, like the female *brevipalpis*, was taken off my person, whilst, without a single exception, the males of *G. brevipalpis* were taken off the path, they making no attempt to attack the party. The second specimen, a female, was taken with two *brevipalpis* during a rest under the heavy shade of trees on the river bank ; the last was caught in more open country to the north of Arusha Chini ; this again was attempting to feed ; it may well have followed the party from the heavier bush of the camp.

Mr. G. W. St. Clair-Thompson's records of this species in the Lake Natron area were much more in accord with the general experience of *G. longipennis*. One specimen was taken near the mountain Burko, on a rocky hill-side, in open scrub with stunted trees of *Acacia mellifera* and probably, according to Mr. Burtt, *A. orfota*, all the country round being open semi-desert grassland ; the fly was caught on a car, anxious to feed, towards 4 p.m. on a hot sunny afternoon. The specimens near Lake Natron were caught in very open scrub with semi-desert grass and dense patches of riverine Acacias along the Ngare Sero stream in which there were permanent pools of water.

Glossina fuscipleuris, Austen.

The Veterinary Department (Annual Report for 1925) were the first to record this species from Tanganyika Territory. The locality, the Sonjo area near Lake Natron, was so remote from any other recorded occurrences that I was for some time sceptical. Mr. Swynnerton, however, knowing the individual responsible for the observation (the late Mr. J. W. Hayes, Veterinary Officer), was confident that the record could be accepted. The recent discovery by Mr. Lewis (1934) of this species on the Mara River in Kenya near our border (which I have shown on the map) supports Mr. Swynnerton's confidence. There is thus little doubt but that *G. fuscipleuris* must be included amongst the tsetse-flies of Tanganyika.

Mr. Lewis' (1934) observations on this species make it obvious that the great eastward extension of *G. fusca* shown by Newstead (1924, Map II) is based on a misidentification, and so this species must be regarded as entirely western and central with its distinct variety, *congolensis*, in the southern part of its range. It is tempting to regard it as the western counterpart of the eastern *G. brevipalpis*, as *G. submorsitans* is of *G. morsitans*, and *G. longipalpis* of *G. pallidipes* ; this would leave *G. tabaniformis*, whose habits and habitats seem very similar to those of *G. fusca*, as the western counterpart for *G. fuscipleuris*. However, these comparisons do not bear too close inspection ; the bulk of evidence suggests that *G. fusca* requires distinctly more forestal conditions than does *G. brevipalpis*, although some observers (notably Almeida & Rebelo, 1927, and Fell, 1912) do record it from more open types of bush. Again the dominating factor governing the distribution of *G. fuscipleuris* seems to be one of altitude, at least in the more eastern part of its range, where it occurs at or above about 5,000 feet (Swynnerton, 1936), whereas *G. tabaniformis* must frequent quite low-lying country, being recorded from the Gaboon coastal regions (Gaillard, 1933).

The discontinuous distribution of this species is not quite so easy of explanation as is that of *G. brevipalpis*, though it must be accounted for in the same way ; for when one considers that a general lowering of temperature must have resulted from the moister conditions of the Pleistocene climate (Moreau, 1935), thus producing at lower altitudes the temperature conditions now prevailing only at 5,000 feet and above, one can see how this discontinuous distribution may well represent the limits of a former more widespread occurrence.

Glossina palpalis, Robineau-Desvoidy.

Zumpt (1935a) has divided this species into three, elevating the original subspecies *fuscipes*, Newst., into one, retaining the original *palpalis*, Rob-Desv., as another, and describing as new a third, *martinii*, Zumpt, from Lake Tanganyika. I am inclined to the opinion that these forms are better regarded, as originally in the case of *fuscipes*, as subspecies of *G. palpalis*, for I think that genitalia showing transitional stages between those characteristic for the various forms are to be found, and especially is this so in the genital plates of the females. I hope, when more material is available, to deal with these points in greater detail in a subsequent paper.

For the present, then, I propose to regard *G. palpalis* as a species of very wide geographical range, which appears as three different subspecies in different parts of that range ; of these, *fuscipes* and *martinii* are the only forms occurring in Tanganyika Territory, where they are confined to the shores of, and rivers draining into, Lakes Victoria and Tanganyika, *fuscipes* on the former and *martinii* on the latter. Their distribution is entirely dependent on the presence of permanent surface water. Zumpt's (1935b) record of this species from Morogoro must have arisen from a mistake on the label (or possibly there is a Morogoro on or near Lake Tanganyika, for there is much duplication of place-names in East Africa), for all the evidence shows that *G. palpalis* is a Western and Central African species, the eastern limits of which are the Central African Lakes and the rivers draining into them ; moreover, fairly intensive fly surveys have been carried out recently in Morogoro and its neighbourhood, which must have revealed this species had it really existed there.

On the map I have given only the actual records of which I know. The species must, however, exist wherever the natural fringing forests of the lake shores and river banks still persist. On the eastern shores of Lake Victoria the extensive clearings carried out by the Germans in their campaign against sleeping sickness have to a large extent been occupied and maintained by the inhabitants, with the result that the fly has ceased to exist over large areas of that coast. On the other hand, a recent flight round the south-west corner of the lake and up the Bukoba coast showed very much more extensive forestation, except when the Bukoba coast was reached, and it is likely that much of that south-western corner is infested with the fly. The shores of Lake Tanganyika between Ujiji and the Belgian border were investigated by Dr. Maclean in 1926 ; from his report it appears that here too *G. palpalis* occurs wherever the natural lake shore and riverine vegetation remains, and that along this stretch patches of cultivation alternate with stretches of fly-infested bush, the latter rather predominating. Of the condition south of Ujiji I have no information further than that afforded by the records obtained by Dr. Maclean at the stopping-places of the Lake steamer ; it is likely that the same state of affairs prevails there, but I am unable to say whether cultivation or fly-infested forest predominates.*

Of particular interest are the records obtained by Dr. Jackson last year on the Malagarasi River some 60 miles inland from the Lake. It is, however, little likely that *G. palpalis* occurs so far inland as this elsewhere, for no rivers flow into Lake Tanganyika of the size of the Malagarasi or with permanent waters stretching so far up their courses ; Dr. Maclean records that the furthest inland he found this fly was three-quarters of a mile, the average being nearer half a mile, on the streams of the stretch between Ujiji and the Belgian border.

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* The latter. It is also definitely known that a great part of the south-western shores of Lake Victoria are infested with *G. palpalis*.—C. F. M. Swynnerton.

I have not been able to examine specimens from Lake Tanganyika within our borders, but the fact that Zumpt's specimens showing the characteristics of *martinii* came from both the south and north ends of the Lake (Zumpt, 1935b) renders it likely that the whole of the Lake is infested with this form. Some specimens collected by Mr. Swynnerton from Kituta, at the south end of the Lake, just over the Northern Rhodesian border, certainly show the characters described by Zumpt for *martinii*.

The confinement of this species to the western and central portions of Africa is not a little difficult to understand, when there is so much of the East Coast, and the large rivers draining into the Indian Ocean, which would appear to be at least as suitable as the shores and rivers of Lakes Victoria and Tanganyika. Under the climatic conditions which now prevail, its failure to reach these eastern haunts is easily explicable by their severance from its central haunts by the large stretches of the East African Plateau which lack anything in the nature of the permanently flowing rivers required by it. At the same time, it might have been supposed that during the moister Pleistocene periods, such water connections might have existed, especially in view of the large extension of Lake Victoria joining up in one huge sheet of water the Eyasi and Wembere systems, now mere seasonal swamps with residual widely separated lakes (Teale, 1931, p. 3). However, rather than postulate that *G. palpalis* has evolved as a species in the central and western areas since so recent a time, it is more reasonable to suppose that even though the moister Pluvial Periods gave rise to climatic and vegetational conditions permitting the spread of *G. brevipalpis* and *G. fuscipleuris*, which are less dependent on surface water, to the limits of their present range, they did not provide the permanently flowing rivers, demanded by *G. palpalis*, continuously enough to allow it to bridge the gap.

Glossina morsitans, Westwood.

A more serious problem is presented by this species than by any of the preceding, not only on account of the huge area of country which it infests, but also because it is not circumscribed to a limited range of vegetation type poorly represented in the country. So widespread is it, that no attempt can be made to represent the details of its distribution by means of symbols. It is particularly associated with vegetation dominated by trees of the closely allied genera *Brachystegia* and *Isoberlinia*, an association which occupies vast portions of the Territory.

There are two main belts of this fly. One, on the west, stretches from the Uganda border, over which it extends for a small distance, to the bottom of Lake Tanganyika, where it is stopped by the highlands of Mbeya and the Livingstone Mountains. Starting in the north as a comparatively narrow strip, the fly-belt rapidly widens, and for most of its length has a width of 400 miles or more. Save for a few naturally open areas, such as the grassy swamps of the middle Malagarasi, and the closely settled areas round the larger towns, such as Tabora, and the larger cleared settlements of the Sleeping Sickness Department's concentrations (Maclean, 1929), *G. morsitans* is spread over this whole area, sometimes sparsely, sometimes densely. The other main belt, on the east, starts below the Usambara Mountains in the neighbourhood of Korogwe and Handeni, and stretches right down to the borders of Portuguese East Africa, through which it again extends to other southern territories, in a belt varying from 200 to 300 miles in width. Here, too, save for the settled towns, the highland areas of the Kaguru and Uluguru Mountains, extensive treeless plains, the closely settled cultivation of rich river valleys, *G. morsitans* infests the whole of this vast area, possibly even in greater numbers than in the western belt.

Here it must be said that the eastern margin of the western belt south of Korongo and the greater part of the western edge of the eastern belt have been assumed to coincide with the edges of the cattle areas, as shown by the Veterinary Department in 1933 ; the western boundary of the western belt between Kigoma and the Bukoba boundary is taken from a map by the Sleeping Sickness Department.

A smaller belt occurs in the Central Province, the history and limits of which have been described by Jackson (1933) ; this belt is spreading rapidly, has lately advanced along precisely the lines which Jackson predicted for it, and will probably be still further extended than is shown in the present map by the time that this is in print. A still smaller belt lies just north of the Central Railway to the east of Manyoni Station ; this too is spreading both northwards and southwards. This belt is thought to have arisen comparatively recently, as a result of carriage of fly from the main western belt by the trains to the suitable patch of bush country it now occupies. Another small belt lies in the Eastern Rift Valley from south of Lake Manyara to Ndareda.

All specimens so far examined from the areas outlined above have presented the characters typical of true *G. morsitans* except for some specimens from the northernmost parts of the western belt (Buhungukira and Bukoba), where this fly occurs in a mesophytic thorn association instead of in its usual vegetation type. In these the abdominal markings and colouring were so atypical as to be very difficult to distinguish from *G. swynnertoni* on external characters (Lloyd, 1935) and one or two of the genitalia have been slightly abnormal. Further study, involving the breeding of hybrids in the laboratory, is necessary to determine whether these specimens are the result of some climatic effect, or of hybridisation, for in these areas *G. morsitans* is overlapped by *G. swynnertoni* or is mixed with *G. pallidipes*, and Dr. Corson (1932) has obtained hybrids between the first two species, and I have had in addition a hybrid from the second two.

As its present distribution shows, *G. morsitans* is entirely independent of water, and being less exigent as to shade and cover than the species previously discussed, shows an adaptation to the conditions now prevailing in East Africa so admirable that it is a little difficult to answer the often raised question as to why it does not occupy the whole of the broad-leaved savannah areas available to it. Dr. Jackson (1933) has discussed this in his description of the Central Province Belt. He suggests that these small isolated belts must be regarded as relics of a former and wider distribution, but refrains from offering any clues as to what factor or factors might have produced this retraction of the tsetse from its original haunts. Two possible explanations have been put forward. One, by Dr. Maclean (1929), suggests that, as a result of the security engendered by strong European rule, a population which had previously been aggregated for mutual defence in close settlements of such considerable size as to exclude the tsetse has lately tended to leave these concentrations and disperse itself more generally through the country. As a result, the abandoned cultivation steppes have given place to savannah woodland, in which, for one reason or another, there has been a lag between completion of the vegetative processes of regeneration and occupation by tsetse, which thus now appears to be spreading into fly-free woodlands which present the appearance of having always been suitable for tsetse. At the same time, the inhabitants, dispersed more generally through the bush areas, have not produced open country of sufficient extent or intensity to drive the tsetse out of its original haunts.

The second explanation is suggested by experience in Southern Africa, where fly disappeared from, or was reduced in, areas it had previously occupied in numbers, at or about the time of the rinderpest epizootic, which during the last decade of the nineteenth century swept through that country destroying not only domestic stock but also certain of the indigenous game animals. The suggestions that rinderpest-infected blood might either kill the adult tsetse or diminish their fecundity have been disproved, first by Duke (1919) in so far as any direct effect on the adults of *G. palpalis* is concerned, and latterly by Carmichael (1933), who has shown that for *G. morsitans* neither suggestion can be maintained. The effect of the rinderpest on tsetse has been discussed very fully by Swynnerton (1936) both in light of the South African evidence and of later experience elsewhere (Duke, 1919, and Kennedy, 1929). He comes to a conclusion very similar to that of Fuller (1923), which is, broadly speaking, to the effect that the result of the rinderpest was to disturb a delicate and complicated inter-dependence of habits and vegetation preferences both on the part of the game and the fly in such a way as to affect the latter adversely. It is also only fair to mention that neither Swynnerton nor Jackson* have been able to obtain definite native evidence of any retreat of tsetse coincident with the rinderpest in Tanganyika, but, as Swynnerton (*loc. cit.*) has pointed out, factors other than rinderpest may upset the delicate balance existing between the tsetse, its food supply and its environmental requirements, so that any such upset may well afford an explanation of its withdrawal from areas which now appear perfectly suited to it.

The origin of these smaller isolated belts has now been discussed ; there remain the two main eastern and western belts. These must be regarded as the eastern and western horns of a vast belt of *G. morsitans* which stretches across Portuguese East Africa (continuous with the eastern belt), through Nyasaland and Southern Rhodesia to the south-eastern portion of the Belgian Congo, thus completing the circle to the western belt of Tanganyika.

G. swynnertoni, Austen.

This species, one of the latest tsetses to be described, although a savannah-haunting fly like the preceding, is far less widespread. It inhabits a drier and more open type of wooding than *G. morsitans*, characterised by trees of the genera *Acacia* and *Commiphora* (Vegetation Map, Swynnerton, 1936), but seems, in the areas in which it has been most studied, to require the presence of small thickets. Originally described from the country surrounding the south-east corner of Lake Victoria (Swynnerton, 1923), it has been found to spread over the northern portion of the Territory through the Eyasi and Mkalama regions right across Central Masai-land, and into the Arusha-Moshi area ; Lewis (1935) has recently described its extension into Kenya. The main belt of *G. swynnertoni* extends from the Musoma area through Eastern Usukuma to Lake Eyasi and Mkalama ; incidentally, the eastern boundary of this belt, not known with precision from fly surveys, is taken again from the Veterinary cattle line (1933). The Mkalama block forms almost a separate belt, for the thinness of the bush strip connecting it across the south end of Lake Eyasi with the main Usukuma fly, as revealed by a glimpse over the area during a recent flight, indicates that the connection is considerably slighter than has been shown on the map ; it is also quite possible that in the comparatively near future this connection will be completely severed in the course of the measures against sleeping sickness in progress in Mkalama, now invaded by this disease. Again, the Masai belt is joined to the Mkalama belt by a very narrow connection, which is now almost certainly broken by the intensive reclamation operations that have been carried out by the tribesmen of Mbulu during recent years. Severed from the main belt by the close settlements of the industrious Wasukuma in the central portions of their land, lies the Shinyanga-Nindo belt described by Swynnerton (1923, 1925). This, by the reclamation clearings since 1922, judiciously utilising pre-existing areas of cultivation steppe and naturally open spaces, has been split into three main blocks, portions of which, too small to be shown on the scale employed, have been again separated and have been and are being subjected to experimental attack, the cumulative results of which have been the gradual wresting of portions of its range from this species and their return to the local inhabitants (Swynnerton, 1936).

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* Dr. Jackson, questioning several old natives of the Central Province after writing his paper (1933). obtained accounts of the rinderpest epizootic there, but there was no general agreement that the tsetse were driven back, much of the evidence being quite to the contrary.

G. swynnertoni appears to have occupied a very great proportion of the country suitable for it. The region east of its boundary in Usukuma probably consists of very open plains, with insufficient tree cover even for this species. Again, to the north of the Masai belt lies an area mainly dry and too open to support fly, though between Meru and Kilimanjaro an extension is taking place which has not been indicated on the map, as no fly survey of that area has been carried out in sufficient detail to permit this. There remain uninfested then only the Iramba Plateau and the country south and east of the Masai belt. The first named is at present under threat of invasion by the fly from below, which has until very recently been prevented from occupying it by the steep scarp walls of the Plateau. The second may be uninfested because the fly have not yet had time to occupy it, though there is a possibility that the country concerned is for the most part too dry and lightly bushed ; this has been suggested by Mr. Hornby. The southern portion of the area is in fact to a large extent more thickly bushed than the fly likes, but it is probable that a network of fly may spread eastwards through suitable patches, and possibly even southwards.

It is tempting to speculate on the relations between these two savannah species, *G. swynnertoni* and *G. morsitans.* The most apparent difference between the two types of country favoured by each may be expressed in terms of light ; *G. swynnertoni* appears to choose bush offering a generally higher degree of light intensity than *G. morsitans* is able to occupy permanently ; incidentally, this may explain the apparent importance of thickets to *G. swynnertoni*, for these would afford the necessary protection which the other species obtains from the general canopy of the woodlands it frequents. Is *G. swynnertoni* then a species which has evolved comparatively recently from *G. morsitans* as a result of this adaptation to more open types of bush ? Such a suggestion must remain in the realms of speculation, but there is this to support it, that much of the country now occupied by this species has only been occupied comparatively recently, as for instance in the Shinyanga area (Swynnerton, 1925), the Mkalama area, Central Masailand, and also its extension into Kenya (Lewis, 1934). The compact and continuous nature of the distribution of this species does not raise the problems which need explanation in the discontinuous and dispersed distribution of *G. morsitans.*

Glossina pallidipes, Austen.

This species is certainly more widely spread than its records on the map would suggest, for it, unlike the two preceding ones, has habits which make it comparatively reluctant to appear to man. Surveys destined to reveal its distribution with any degree of certainty require bait cattle, whereas both *G. morsitans* and *G. swynnertoni* attack man so much more readily that such adjuncts are not needed. An outstanding example of the difficulty in discovering the distribution of this species is afforded by the experiences of the South African Government in the Ntabanana settlements of Zululand (Bedford, 1926), where cattle had been dying of nagana for some time, whilst more than one investigation of the area failed to reveal any tsetse ; and so the matter remained as an example of trypanosomiasis of stock occurring outside tsetse areas, until Bedford investigated the area with bait animals, finding his first tsetse, a specimen of *G. pallidipes*, only after about 30 days. A further example of how this fly fails to appear to man in anything like its real numbers is given by Swynnerton (1933), who records how a trap, baited with a calf, caught 584 flies (mainly *G. pallidipes*) in under 6 hours, in a locality where man alone in a similar period would have been lucky to take 6 specimens. This difficulty in detecting *G. pallidipes* led the Veterinary Department at Mpwapwa to attach a greater importance to indirect transmission than it deserved, at least in that instance, until the presence of the species was definitely established by the Tsetse Department in 1932 (see Veterinary Reports for 1932 and previously). Such experiences as these raise the suspicion that many insects regarded as rare and local may really exist in far greater numbers than is supposed, but escape the attention of investigators on account of some little peculiarities in behaviour and predilections which prevent their contact with man. A further instance of this is afforded by that large and handsome Tabanid, *Tabanus guttatus*, which, whilst wide-spread throughout this Territory, never appears particularly abundant ; this I understand from Dr. Lamborn was also his experience in Nyasaland until he discovered its remarkable pupal " cocoons " in dried mud (Lamborn, 1930), when he found that in its pupal state at any rate the species was abundant.

The recorded localities for *G. pallidipes* are so numerous that I shall make no attempt to give a detailed list, and shall do no more than indicate the general areas in which it is to be expected, and comment on certain interesting occurrences and absences. The species is again a fly adapted to life in the savannahs, but requires more thicket shelter, or rather more extensive thickets, than does even *G. swynnertoni*. At the same time, its habit of wide ranging through very open country is responsible for conflicting records of it as an open country fly. Altogether, it is probably the most successful of all the tsetses, both in the extent of the area which it has occupied (for though *G. palpalis* might appear to cover more country, yet it must be remembered that it is by no means universally spread throughout that country, but is limited to linear strips along the lake-shores, rivers and streams), and in the extreme types of country in which it is able to exist. For not only does it frequent comparatively moist highland areas such as the Usambaras, but also it has been found in almost desert country to the north of Handeni by Mr. Burtt, and below the Pare Mountains by Mr. Swynnerton, in which it is doubtful whether even *G. swynnertoni* could survive. In addition, it ranges widely through the territories of both *G. morsitans* and *G. swynnertoni*, whilst its geographical range extends from Italian Somaliland (nearly as far north as any tsetse except *G. morsitans*) to Zululand, well south of most species. It is found from sea-level in the coastal regions to at least 6,000 feet in the Mbulu Highlands (Burtt), where it was definitely established, and where *G. swynnertoni*, which lived with it at lower altitudes, could not establish itself.

G. pallidipes is widely spread throughout the Bukoba *morsitans* areas, as has been shown by recent surveys of Mr. S. Scott, of the Sleeping Sickness Department, and Messrs. Napier-Bax and Lloyd, of this Department. The next occurrence is at the south-west corner of the Lake in the Saragura area just inland from Nungwe Bay, where gold is now being found ; Mr. Napier-Bax caught there four specimens, and later eleven more have been sent me by Mr. Hockley, Hygiene Officer to the Company developing that area. It reappears again in the *morsitans* areas round Kahama. It is interesting that in the course of sleeping sickness investigations in the Ushirombo area to the west of Kahama, Dr. Fairbairn, who dissected over a thousand flies, failed to note a single example of this species amongst the *G. morsitans* of that area ; it is just possible that this may have been due to the investigation having been carried out at an unfavourable time of year. From the great southern portion of the western belt there exist no records of *G. pallidipes* ; Dr. Jackson has carried out extensive investigations in the neighbourhood of Kakoma, some 60 miles south of Tabora, without finding it, and it is probable that, at any rate so far as that area is concerned, a poverty of thickets is sufficient explanation of its absence.

The *swynnertoni* areas of Musoma are again infested with the species, which, with *G. brevipalpis*, also occurs outside them in country containing thicketed streams and clothed with a broad-leaved savannah unsuitable for *G. swynnertoni*. Isolated records from the Sengerema extension of the main *swynnertoni* belt (on the extreme west, in the neighbourhood of latitude 3°S.) and again near the Simiyu (Vicars-Harris and the writer) a little to the north of this, link up with its occurrence in the Nindo-Shinyanga area (first recorded by Mr. Swynnerton, 1925), which again is probably continuous with the Kahama occurrences. The Sengerema experience is an interesting one, for a few specimens were found by Messrs. Swynnerton and Napier-Bax in their initial survey of the area, but none was ever again found during a period of over two years of regular fly-rounds in the area, every fly of which was examined by me personally.

In the main Usukuma-Mkalama belt, no records of *G. pallidipes* exist, although many specimens of *G. swynnertoni* have been examined from the neighbourhood of the Simiyu River near Maswa, to the east of the Sengerema record, in country where one would expect the species to occur, especially in the light of the record from lower down the river. At the same time, extensive areas between Maswa and Lake Eyasi, as seen from the air, appear very thicketless, although it is true that they are traversed by thicketed rivers.

The species is not again met with until the south-west slopes of Oldeani are reached (Burtt), and thence is frequent throughout the Mbulu Highlands to the Eastern Rift Valley, along which it spreads both northwards and southwards, mixing with both *G. morsitans* and *G. swynnertoni*.

The Central Province *morsitans* belt, from which many thousands of flies have been examined by members of this Department from time to time, is quite free from *G. pallidipes*, except for one specimen taken at Kikori by Mr. Lloyd towards the end of a series of very intensive investigations of that area in which a number of different people were engaged. It is doubtful whether this record of a single specimen can be regarded as indicating establishment of the species there, as it was quite possibly a stray fly carried in from the mixed belt to the north-west by a car ; at the same time, I should consider the country quite suited to the species, and it will probably be only a matter of time before it does definitely become established, at any rate in that corner of the belt.

The next area to be defined is that around Meru and Kilimanjaro, extending to the North Pares ; Mr. Swynnerton took it in some numbers in the Northern Pare Game Reserve, between the Pares and the Pangani River, and the species is probably spread through the South Pares and the North Usambaras, but no further definite records exist until the South Usambaras are reached. It is probably far more common throughout the great Eastern *morsitans* belt than is shown by the records, and its existence just outside, north and east of Handeni, has been referred to before.* Another extension outside the belt, again on its eastern margin in the neighbourhood of the Central Railway, occurred in the country just north of the railway, and was threatening the Veterinary Headquarters and Experimental Station at Mpwapwa ; however, timely reclamation measures undertaken on the advice of the Tsetse Department would appear to have removed the menace (Annual Report of the Veterinary Department, 1934).

The records for the southern part of this great belt are confined to two, but this has been so inadequately surveyed, that these two, so widely separated, suggest that the species is in reality widely dispersed over the area ; incidentally, the nature of the vegetation renders this much more likely than in the corresponding area of the western belt.

Mr. Burtt (Veterinary Annual Report, 1932) caught a specimen of *G. pallidipes* on the railway station at Dodoma, on the Central Railway, right in the middle of the uninfested third of the Territory. This has not been placed on the map, since Dodoma cannot be regarded as really fly-infested on the strength of a fly carried into it by a train ; were this to be accepted, the whole of the railway line through the fly-free portion of the Territory must be shown as infested with *G. morsitans*, *G. pallidipes*, and even *G. brevipalpis*, for few trains can fail to carry through it many specimens of one or more of these species picked up in the fly-belts on each side, and naturally at any halt such flies are liable to descend. The nature of the country, however, is such that it is unlikely that any of them so dropped will survive long enough to establish a colony. At the same time, occurrences at Dodoma are deemed sufficient by the Veterinary Department to account for the cases of trypanosomiasis which occur there from time to time (*loc. cit.*).

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* It is very common in all the country north and south of Kilosa, extending thence to Dar-es-Salaam and south of this place at least to the Rufiji near Utete. I have taken it personally in many localities in this area. I have had long series of flies from various localities in the Mahenge and Lindi Provinces, from Messrs. Hodgson and Lawrence. They have mostly been *G. morsitans* with a very few *G. pallidipes*.—C. F. M. Swynnerton.

Glossina austeni, Newstead.

This fascinating little species of tsetse, originally recorded from Kenya as *G. tachinoides*, and actually described as a new species (*G. brandoni*) from Zululand, has subsequently been found at many places along the East Coast, and even far inland. It, more than any other tsetse, appears reluctant to obtrude itself on the notice of man, and survey with bait cattle is essential in areas in which it is suspected ; it is just possible that this reluctance may be due to an extreme specialisation in the host preferences of the species. Mr. Moggridge, of this Department, has taken its pupae in considerable numbers in a locality where he failed to find a single adult specimen without bait cattle. Much information on the habits of this little-known fly has been collected by Mr. Swynnerton (1936), who has been himself responsible for much of our knowledge regarding it. He describes it " as a fly probably less far ranging and adventuresome than *pallidipes* but much more so than *brevipalpis* is by daylight ; as a fly which, like *pallidipes*, bases itself on fairly dense thicket, whether extensive (but broken) or scattered, and breeds therein, but sallies to seek for its food into country devoid of undergrowth, or with open spaces interspersed, outside the thicket " (Swynnerton, 1936).

Briefly, *G. austeni* is known in this Territory from the Southern Usambaras, the Nguo Mountains near Handeni, the Coast between Pangani and Bagamoyo, the flatter country north and south of Kilosa and the Kaguru foothills near there, the Ngerengere River near Morogoro, south of the Ulugurus, and near Kidete on the Central Railway, and has been found, too recently to include in the map, on the coast between Kilosa and Lindi. The anomalous characters of this most interesting species prevent the writer from offering any further comments as to the reasons for its present distribution.

5. The Fly-belts of the Territory.

A short outline of the fly-belts, with their constituent species, will serve to summarise the details given in the preceding section. They are eleven in all :—(1) The Great Western Belt, (2) the Musoma-Usukuma Belt, (3) the Eyasi-Mkalama Belt, (4) the Rift Valley Belt, (5) the Central Province Belt, (6) the Hika Belt, (7) the Masai Belt, (8) the Natron Belt, (9) the Pare-Usambara Belt, (10) the Great Eastern Belt and (11) the Rungwe Belt.

(1) *The Great Western Belt.*—This, occupying nearly one-third of the Territory, stretches from the Uganda border to the south end of Lake Tanganyika, narrow at first, but widening out south of Lake Victoria to well over 100 miles, and finally in its southern half stretching over more nearly 400 miles of country. Over this vast area *G. morsitans* is generally distributed ; *G. pallidipes* is recorded from its narrow northern section, at the south-west corner of the Lake and again near Kahama ; *G. palpalis fuscipes* occurs round the south-west corner of Lake Victoria, and the subspecies *martinii* along the coast of Lake Tanganyika, and up the streams and rivers draining into that lake, generally for less than three-quarters of a mile, but occurring at least 60 miles inland on the great Malagarasi River. *G. brevipalpis* occurs also, possibly in Bukoba and certainly in the Kigoma area. This belt overlaps slightly outlying severed portions of the second belt (of *G. swynnertoni*) in the Buhungukira, Shinyanga and Manyonga sections.

(2) *The Musoma-Usukuma Belt.*—This smaller northern belt occupies the southern and eastern portions of Musoma and stretches southwards through eastern Usukuma to the Manyonga-Kenworthy-Eyasi system of swamps and lakes. It is separated from the small outlying belts of Buhungukira, Nindo-Shinyanga, and the central Manyonga by the Central Usukuma Cultivation Steppe ; a small belt in the south-west, Kitalala, has also been cut off by reclamation clearing. The area is occupied throughout by *G. swynnertoni*, with *G. brevipalpis* and *G. pallidipes* on its northern margins. A small focus of *G. pallidipes* also occurs on its western edge just above 3°S. North of it is a scattered infestation of these two species, with *G. palpalis fuscipes* on the Lake shores and stretching up some of the rivers ; this infestation does not preclude the maintenance of a flourishing cattle population.

(3) *The Eyasi-Mkalama Belt.*—Connected with the preceding by a narrow neck of thin, fly-infested bush south of Lake Eyasi, this belt, consisting entirely of *G. swynnertoni* except in its northern and north-eastern corners, occupies the Eyasi Basin, the Hohenlohe Rift and an extensive bush area between that and the Mbulu highlands ; it is threatening the Iramba Plateau by ascent up river valleys which dissect the Plateau Scarp. *G. pallidipes* occurs at its northern and north-eastern corners, probably connecting thence through the Mbulu Highlands with the fourth and sixth belts.

(4) *The Rift Valley Belt.*—This is a small belt of mixed *G. morsitans* and *G. pallidipes* lying along the foot of the Eastern Rift Scarp, and occupying the width of the Rift Valley between Lake Manyara and a higher portion of the valley which intervenes between that Lake and the great extinct volcano, Hanang.

(5) The *Central Province Belt.*—This, a belt of pure *morsitans* (except for the record of a single specimen of *G. pallidipes* in its north-east corner, probably a mere stray) occupies on the east a narrow stretch between the bottom of the Irangi Scarp and the Masai plains ; from this a thin neck crosses a narrow highland strip, the Bereku Ridge, through the agency of interdigitating valleys, to the Usandawe country, which it has invaded during recent years, and from which it now threatens the populous Singida country ; across this, if unimpeded, it is likely to join with the first belt, and possibly also the sixth.

(6) *The Hika Belt.*—This is a small belt, probably of comparatively recent origin, lying to the north of the Central Railway just east of Manyoni Station ; consisting entirely of *G. morsitans*, it shows signs of expanding, chiefly in a northern direction.

(7) *The Masai Belt.*—Composed entirely of *G. swynnertoni* except for scattered *brevipalpis* (and probably *pallidipes*) in its extension towards Arusha and Moshi, this belt occupies the western and northern parts of Central Masailand, with an extension of its north-west corner up along the Eastern Rift Valley, where also it is mixed with *G. pallidipes.*

(8) *The Sonjo-Natron Belt.*—This occupies the top of the Rift Scarp west of Lake Natron ; its southern corner is known to contain *G. pallidipes* and *G. longipennis*, and somewhere in it *G. fuscipleuris* must occur, but its general constitution is not known with certainty. In all probability, it is mainly infested with *G. pallidipes* (an extension from Kenya), with a general scattering of *G. longipennis*, and *G. fuscipleuris* in suitable stream-beds.

(9) *The Pare-Usambara Belt.*—This belt in its northern and southern portions consists of scattered *G. brevipalpis* and *G. pallidipes*, with the addition of *G. longipennis* in the north and *G. austeni* in the south. It is probably mainly, and throughout its middle portions as well, infested with the first two species. It is of interest because in the Veterinary Department's Cattle map this area figures as maintaining a cattle population, albeit of a lower density than it is capable of supporting. In other words, it looks as if in this area at least infestation by these more localised species is not incompatible with a cattle population, though at a lower level than in

completely fly-free country. Although the cattle are only kept, according to Mr. Swynnerton, in the fly-free stretches between the infested areas, I do not think that they could live in such patches among areas infested with the savannah species of tsetse—*G. morsitans* and *G. swynnertoni.*

(10) *The Great Eastern Belt.*—This, nearly approaching the Western Belt in size, is infested almost throughout with *G. morsitans* and probably more locally with *G. pallidipes* and *G. brevipalpis.* In addition, *G. austeni* occurs in its northern portion to a point a little south of Kilosa, and again on the coast further south, where the Kilosa and Lindi Districts meet. This belt stretches from south of the Usambaras to the Portuguese border, and varies from 200 to 300 miles in width.

(11) *The Rungwe Belt.*—This is merely a small area infested with *G. brevipalpis* at the north end of Lake Nyasa.

6. Some Natural Features affecting the Distribution of Tsetse-flies.

A striking point in connection with *G. morsitans* is the extent to which its distribution coincides with that of Miombo (*Isoberlinia-Brachystegia* wooding), which is never invaded to any extent by *G. swynnertoni.* Mr. Swynnerton originally called attention to this in his map (Swynnerton, 1925) of the Shinyanga area, and his early generalisation has been justified so far as Tanganyika Territory is concerned (see also Swynnerton, 1936, for greater detail). It is of course recognised that *G. morsitans* does occur over large areas dominated by other types of vegetation, such as the *Copaifera mopane* wooding of Rhodesia and Nyasaland. In the case of such occurrences outside Miombo in Tanganyika itself the vegetation concerned is always either some type of Mesophytic Thorn association (Swynnerton, 1936—*e.g.*, the *Acacia hebecladoides* associations of Bukoba, or the *Acacia pallens* woodlands of Kilosa), flourishing under definitely moister conditions than do the Dry Thorn associations favoured by *G. swynnertoni*, or a broad-leaved community dominated by trees of the genera *Ostryoderris* and *Combretum*, which again produces an effect a little similar to Miombo. Lloyd (1936) describes in detail the relations which he found to exist between *G. morsitans* and these associations in Bukoba and Buhungukira, and shows that, just as in Miombo, certain elements of the associations have their peculiar significance for the different phases of the tsetse's activities.

The coincidence of a particular species of fly with a particular type of vegetation is not conceived as being due to any direct association between the species of fly and particular species of trees. Rather does it arise from a combination of the two following causes—(*a*) that the climatic conditions resulting in a particular vegetation community are just those favouring a particular species of tsetse, and (*b*) that the general conditions resulting from the vegetative cover of a particular type are just those which suit the particular fly. In other words, that the species of fly and the vegetation community alike are two modes of expression of a particular climatic complex.

The uninfested portions of the Miombo will probably all become infested in time, for none are sufficiently separated from each other for fly to be unable to bridge the narrow stretches of thorn country between. Exceptions to this are possibly the Miombo of the Iringa country, and certainly the small area of peculiar Miombo on the Kondoa Plateau, across which the small *morsitans* belt under the Irangi Plateau connects with the main Central Province Belt through scantily infested interdigitating valleys. This Miombo consists very largely of fine old specimens of *Brachystegia microphylla*, which association on the lower slopes of the scarp is of peculiar importance to *G. morsitans* (Nash, 1930, 1933) ; it is not, therefore, any peculiarity of vegetation that prevents the fly from occupying this particular woodland. That it is so prevented is almost certain, for we have known this area since 1928, and in spite of the presence during all this time of numerous tsetse below the scarp, there is even now, according to Captain Findlay, who is now working in this area, no sign of any general infestation of the *microphylla* wooding at the top of the plateau. He further tells me that he finds fly infestation to cease at about 5,000 feet there, although odd flies will follow a party or be carried by game above that altitude. It would therefore seem reasonable to ascribe the freedom of this *microphylla* to its altitude, for most of it lies between 5,000 and 6,000 feet ; presumably some temperature or even humidity effect is concerned, for altitude *per se* cannot be conceived as limiting the fly (see Moreau, 1934, pp. 44–47, for a discussion of this subject). The conception then of altitude as a convenient way of expressing an undefined complex of climatic and vegetational factors must be kept in mind when figures of altitude are quoted below. How far the decreasing atmospheric pressure and oxygen content at high elevations may affect tsetse is another question ; such scanty experimental evidence as is available from insects in general suggests that such pressure differences as are likely to occur at the greatest altitudes normally available to tsetse are unlikely to affect either the insects themselves or their developmental processes (Uvarov, 1931, p. 78).

This then leads to the next feature to which I wish to draw attention, namely, the limiting of fly-belts by topographical features such as mountain blocks and rift scarps. Thus, the arrest of the Mkalama *swynnertoni* at the foot of the Iramba Plateau is obvious. Such an arrest is not necessarily permanent, and probably is not so here, where the presence of fly on the top of the scarp has recently been reported, and where the vegetation of the top of the plateau is probably suitable, and the altitude not great enough to be likely to produce unfavourable climatic conditions. In other areas, as for instance the two northern belts of the Eastern Rift Valley, the arrest is likely to be permanent. There, although a few flies (both *G. morsitans* and *G. swynnertoni* in their respective zones) do succeed in reaching the top of a rift scarp so precipitous that it might be thought to serve as a barrier in itself, yet the climatic or vegetational conditions (or both) on the top are so unfavourable that these flies never do succeed in establishing themselves permanently. The climbing of such scarps is probably mainly performed by hungry flies which follow man or game up their paths, although it is sometimes caused by flies driven in front of grass fires which sweep through the fly-infested bush at the bottom and on up the scarp. The third belt of the Eastern Rift Valley, the south-western portion of the Central Province Belt (No. 5), faced by less precipitous slopes and with favourable vegetation on top of the scarp, which is lower there, is now establishing itself on the top, and unless last minute efforts at stopping it succeed, will spread over large areas there. In the south, the main Eastern and Western Belts seem to have come up against limiting mountain blocks in the Ufipa and Mbeya Highlands, the Livingstone Mountains, and the Songea, Iringa and Usagara Highlands ; I have not sufficient knowledge of these areas to hazard any remarks as to the permanence or otherwise of this state of affairs.

The above instances show that these topographical features limit tsetse by virtue of an associated change, sometimes in vegetation, sometimes in climate, or in both. Though rift scarps sometimes delay an advance of fly, they probably never completely stop it unless the conditions at the top of the scarp are so changed as to be unsuitable to the fly at the bottom. It would seem that, generally, in Tanganyika neither *G. morsitans* nor *G. swynnertoni* can exist permanently at much over 5,500 feet, though it is possible that so near the equator as the Bukoba area this limit does not hold. It is very difficult to generalise on the elevation at which a species is capable of existing ; doubtless much depends on the latitude, for Jack (1927), in Southern Rhodesia, is of the opinion that *G. morsitans* is limited there to 4,000 ft. and below ; in those parts of Africa nearer the Equator, approximately 5,000 feet is more generally given (Newstead, 1924, p. 195) ; such an increase in altitudinal range nearer to the Equator is, I think, to be expected. Again I would emphasise in the words of Moreau (1934, p. 47) that " altitude expressed in feet or metres is best regarded as nothing more than a convenient shorthand method of indicating a complex of meteorological and biological conditions which invariably require to be defined for the particular district considered."

The last feature to which I wish to draw attention is the effect of those peculiar blocks of thicket, known as the Itigi Thickets (Phillips, 1930, p. 357), and situated mainly in the Central Province on and north of the railway near Manyoni. These form a very distinct and peculiar vegetation community, a knowledge of the detailed constituents of which we owe to Mr. Burtt ; this community has probably existed from ancient times and is no recent effect of man's activities, for its plants number several endemic species, and one endemic genus ; it is apparently limited by a peculiar type of soil and underlying rock (Gillman, 1936a). These thicket blocks have turned the eastward movement of the great Western Belt northwards, so only just now after a delay of 9 years it is sweeping again eastwards round the northern tip of the thicket blocks. The fly reached these thicket blocks in 1927, when hopes were entertained of stopping this northward turning movement, and so ending all advance in that sector, by means of a barrier clearing from the thickets to the open grasslands of the Wembere Swamp, which, continuing indefinitely northwards through the Serengeti Plains over the Kenya border, offered a magnificent natural barrier ; unfortunately these hopes were frustrated, and the fly is now advancing by leaps and bounds through the uninfested Miombo west of Singida, and threatens to turn eastwards and southwards again to join the Hika Belt.

7. Possible Extensions of the Fly-belts.

The fly-free country which is likely to be invaded has been indicated, but a brief summary may perhaps give a clearer picture of what further loss of cattle country the Territory may have to face. The Western Belt is likely to extend further into the area west and north-west of Singida ; again, an eastward filtration round the top of the thicket, south of Singida, will give it the opportunity for southward extension to join a northward spread of the Hika Belt (No. 6), from which coalescence a further eastward movement would meet the westward advance of the Central Province Belt (No. 5) envisaged by Dr. Jackson (1933). Meanwhile the threat to the Iramba Plateau, mentioned on p. 137, would, if successful, complete the encircling of the Singida Cultivation Steppe by tsetse.

There appears to be nothing to stop the southern edge of the Central Province Belt from spreading, on the one hand, south along the eastern face of the Great Thicket and thence eastwards across the narrow valley of the Bubu to occupy the Miombo of the Chenene Hills, and on the other hand towards the south-east into the Burungi country. The greatest possibilities of extension of the Masai Belt (No. 7) seem to me to lie in an eastward movement of its southern extremity, which would eventually turn southwards round the Burungi country between Kondoa and Kibaya, and such a thrust might even reach the Central Line west of Mpwapwa, throwing off on its way a backward (westward) tongue to over-run large stretches between Kondoa and Dodoma. It is not outside the bounds of possibility that the whole of the eastern boundary of this belt might extend at least as a net-work over Central Masailand to the Ruvu Valley, and even its northern bounds be produced as a lacework of fly-infested country over the scanty patches of bush of northern Masailand. Should these advances take place, there will remain but little of the Territory uninfested.

In addition to such occupations of fly-free country as have been described above, it is possible that a certain amount of overlapping may occur still further, in particular of *G. pallidipes* with both *G. swynnertoni* and *G. morsitans* ; though if our present views on the factors which limit these last two species are correct, no considerable overlapping between them is likely. The practical importance of such an overlapping by *G. pallidipes* or any other of the more localised species would be a complication of the problem of reclaiming such country, for methods applicable to one species are not always effective against another.

In two very interesting and thought-provoking articles (Gillman, 1936, p. 6, and 1936a, p. 13) the view has been expressed that water-supplies are the paramount factors in determining the distribution of the human population of Tanganyika Territory, and it has been rather implied that the abandonment to the tsetse of areas in which the water-supplies are not sufficient to support a population of fly-excluding density should be regarded as a just tribute to an insect so much better adapted than man to occupy those semi-arid parts. Apart from questioning whether the tsetse is not actually capable of turning people out of even the most adequately watered areas, and experience in Shinyanga suggests that it does in fact do this (Swynnerton, 1925, pp. 318, 319), I consider that the mere fact of the minute size of those areas of the country, as estimated by Mr. Gillman himself, which are so well watered as to allow of occupation by population of fly-excluding density, emphasises the paramount importance of seeking and applying any methods which will dispossess the tsetse of the vast though poorly watered areas which could then be made available for human occupation, and so relieve the intolerable pressure of human population on the limited well-watered areas which are being so rapidly impoverished.

So gloomy a picture of an ever advancing tsetse has been drawn, that the question must arise—" Does the fly never naturally retreat ? Is there no rhythmical ebb and flow of the fly belts ? " Tsetse do retreat naturally, we know ; recent experiences in the Ankole belt in South Uganda (Simmons, 1929, p. 423) show this, whilst the great contractions of fly-belts following on epizootics of rinderpest have been already discussed. It does, however, seem that present conditions in Tanganyika are such that tsetse are almost universally advancing. Even here there are suggestions that country has been abandoned by the fly during the last couple of decades, but these are seldom well enough documented to allow any certainty as to whether seasonal fluctuations such as have been described by Jackson (1930, p. 504) and Nash (1930, p. 255, and 1933, p. 132) have not been mistaken for more permanent withdrawals. One cause of such natural retreats—epizootic rinderpest—has been discussed ; others may well be imagined. For instance, should an especially unfavourable season, such as the very heavy rains of 1929–30 in Kikori (Nash, 1933, p. 113), have occurred in country less well suited to the fly, the great reduction in numbers described might well have become at least temporary extinction. Again, apart from sudden changes in the vegetation caused by catastrophic events such as volcanic eruptions, slow changes may well render suitable country unsuitable. Were an organisation available for discovering any such natural checks to the fly as soon as they occur, these might easily be rendered permanent, and thus large areas recovered with a small expenditure of effort. Such an organisation would demand as its basis exact knowledge of the existing distribution of the tsetse, so that even the detailed study of fly distribution has its practical bearings.

8. Summary.

1. Details are given of the distribution of the eight species of tsetse occurring in the Tanganyika Territory (*G. brevipalpis*, *G. longipennis*, *G. fuscipleuris*, *G. palpalis*, *G. morsitans*, *G. swynnertoni*, *G. pallidipes*, and *G. austeni*).

2. The effect of past climatic changes on the present distribution of some of the species is discussed in a somewhat speculative manner.

3. The detailed information is summarised in a general description and map of the fly-belts of the Territory.

4. The effect of certain broad vegetation types and major topographical features on the distribution of species of tsetse in Tanganyika are discussed.

5. The effect of the major topographical features in limiting the distribution of the fly is always found to reside in some accompanying vegetative or climatic feature.

6. Possible and likely extensions of the fly-belts are briefly indicated ; if these should take place, but little of Tanganyika Territory would remain uninfested by tsetse-fly. The possibility of natural retreat of fly-belts is also discussed.

7. A few details are given of the habits and habitats of some of the lesser known species (*G. longipennis, G. fuscipleuris* and *G. austeni*).

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* Paper not seen, quoted from Moreau (1933).

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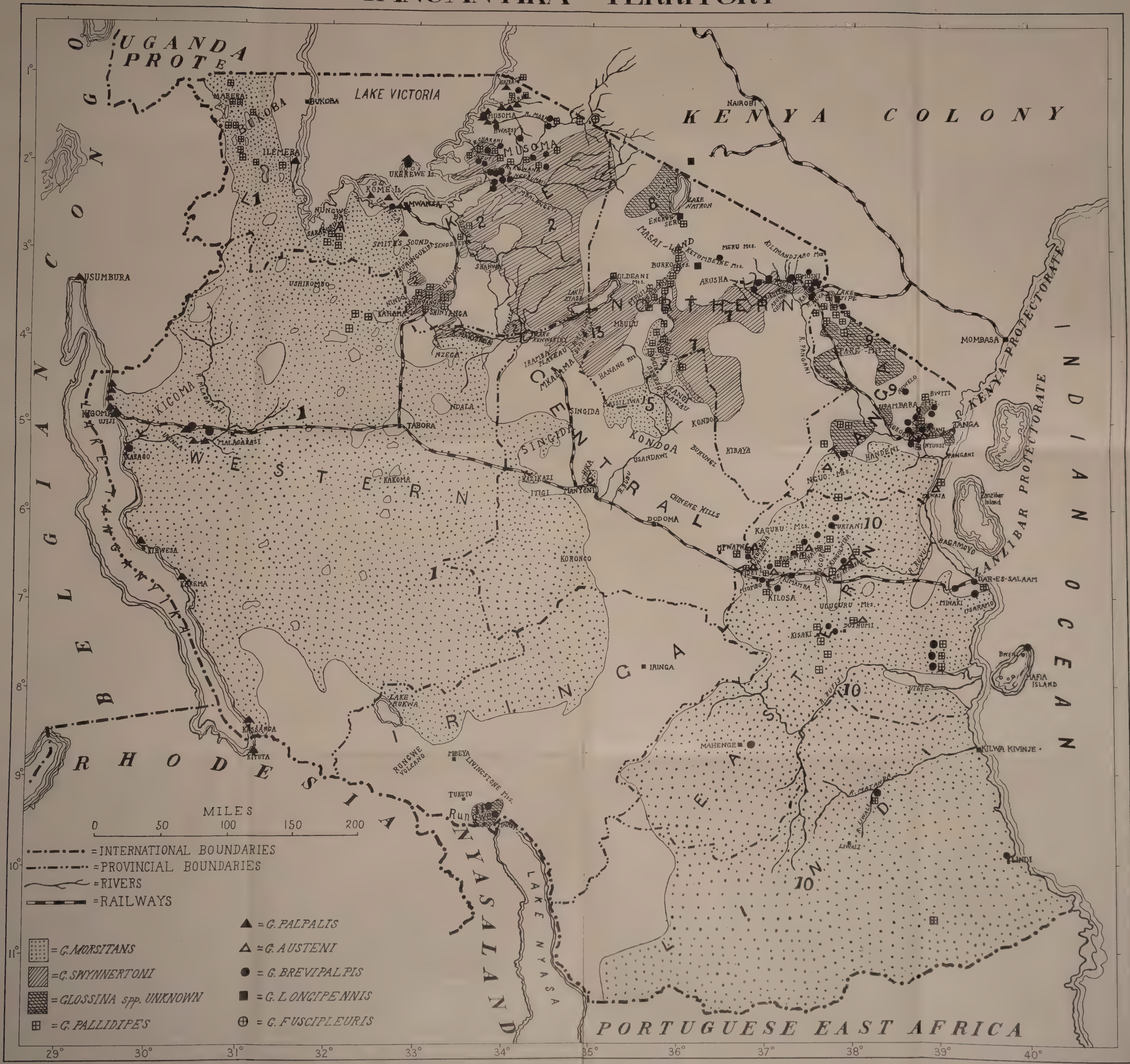
TANGANYIKA TERRITORY


UGANDA PROTE
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LAKE VICTORIA
LAKE TANGANYIKA
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NUNGWE BAY
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MPWAPWA
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DAR-ES-SALAAM
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KILIMANJARO Mt.
MERU Mts.
KETUMBEINE Mts.
ENGARE SERO
OLDEANI Mts.
MBULU
HANANG Mt.
IRAMBA PLATEAU
MKALAMA
KIBAYA
USANDAWI
BURUNGI
CHENENE HILLS
NGURU Mts.
KAGURU Mts.
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KISAKI
DUTHUMI
MINAKI
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MBEYA
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RUNGWE VOLCANO
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=RAILWAYS
=G. MORSITANS
=G. SWYNNERTONI
=GLOSSINA spp. UNKNOWN
=G. PALLIDIPES
▲ =G. PALPALIS
△ =G. AUSTENI
● =G. BREVIPALPIS
■ =G. LONGIPENNIS
⊕ =G. FUSCIPLEURIS

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OBSERVATIONS ON THE MORPHOLOGY AND BIONOMICS OF *SERICA BRUNNEA*, L., WITH NOTES ON ALLIED CHAFER PESTS.

PART I.

THE MORPHOLOGY OF THE LARVA OF *SERICA BRUNNEA*, L.

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Introduction.

It is a remarkable fact that out of the six commonly occurring species of the family SCARABAEIDAE (chafers, white grubs) in Britain, five are constantly reported as causing damage, either as grubs or as adults, to agricultural and forest crops. Thus, of the six species listed in Table I, only the last named, *Anomala aenea*, de Geer, which is very abundant locally on sand-dunes, finds agricultural conditions unsuitable to its existence.

TABLE I.

Species	Life cycle (years)	Authority	Occurrence of larvae in Britain
Melolontha melolontha, L.	4	Decoppet 1920 Munro 1927	Arable land Market and flower gardens Forest nurseries
Rhizotrogus solstitialis, L.	3		Market gardens Forest nurseries
Serica brunnea, L.	2 (and 3 ?)	Munro 1927	Forest nurseries Stabilised sand-dunes
Phyllopertha horticola, L.	1	Rittershaus 1927 Taylor & Thompson 1926	Grassland Orchards (adults) Forest nurseries
Cetonia aurata, L.	3 (?)	Fryer 1928	Rose gardens (adults) Arable land
Anomala aenea, de Geer	2	Rittershaus 1927	Sand-dunes Sandy woodlands

It is surprising to find that, despite the economic importance of the group, its bionomics have been left practically untouched by British writers, and in the case of *Serica brunnea*, L., which forms the principal subject of this paper, its status, as one of the worst pests of forest nurseries, remained undiscovered until the work of Munro (1927). This is, in part, due to the practice common in the past of classing the larvae of these forms in a group as " white grubs " without any serious effort to fix the identity of the species. It is only recently that attention has been paid to this question in America (Hayes, 1929), where the problem is complicated by the existence of more than 50 species of the genus *Lachnosterna*, which are of economic importance, and by the presence of important species, notably *Popillia japonica*, Newm., *Aserica castanea*, Arr., and *Anomala orientalis*, Waterh., imported from the Far East.

The present paper can only claim as its groundwork a year of observation in the field, supplemented by rearing experiments and morphological work in the laboratory. This was carried out at the Field Station of the Imperial College of Science and Technology at Slough, during the first year of a Ministry of Agriculture Research Scholarship, and the writer takes this opportunity of expressing his thanks to Professor J. W. Munro for his constant help and encouragement.

Material and Methods.

Although *Serica brunnea* occurs quite commonly in sandy areas, its larva is seldom found in concentrations sufficient to enable a study of its habits and structure to be made. As a pest, it is entirely confined to forest nurseries, where it causes great damage by gnawing the roots of seedlings and transplants, chiefly those of conifers. Through the kindness of Dr. R. N. Chrystal, access was obtained to Forestry Commission nurseries in the Forest of Dean, where many valuable field observations were made, and the bulk of the material was collected.

The larvae were transported to Slough in large tins, well packed with slightly damp sphagnum moss. In this way only a small mortality resulted, due to the larvae biting each other. Rearing was carried out by numerous methods, the most successful of which was the subterrarium. This is a modification of apparatus described by Willaume (1924, 1927–29) and consists of a pair of well-supported wooden uprights, rebated to take a glass plate on each side, these being retained in position by means of four metal clips, leaving a soil space between them of two centimetres, for the *Serica* larvae. The lower cross-pieces are set apart and spanned with perforated zinc to ensure adequate drainage. The upper cross-piece serves as a handle, which renders the whole plate easily transportable. If the plates are to be kept in the light, a piece of sheet zinc is inserted under the clips in order to obscure one side, to which most of the larvae will eventually move, enabling them to be observed with greater ease. The plate is filled, at the bottom, with broken pot, then with a few inches of clean sand, and finally, with a light sandy loam, which will retain sufficient moisture and be of a suitable texture to enable the larvae to form their cells. The larvae are placed on the soil surface, where they readily burrow.

The above method is especially successful for fully fed larvae in order to observe winter and spring movements and pupation, and although feeding has been carried out by means of germinating wheat grains placed under the glass, the method becomes laborious, since the amount of food taken is very great.

Rearing in boxes of lettuce plants is then more convenient, or, for individual observations, the method of Davis (1916), of isolating larvae in 1 oz. vaseline tins, has been successfully used.

The most serious problem in rearing soil insects is the retention of sufficient but not excessive humidity. For this reason, the only satisfactory method is to construct an underground cave, in which all rearing apparatus can be placed. For this purpose, a hole 5 feet by 5 feet by 5 feet was dug, and roofed in by means of a section of iron fencing covered with corrugated iron and banked over with grass sods. A trap-door and entrance steps completed the main chamber. A side chamber was constructed, 2 feet by 2 feet by 3 feet, and lined with perforated zinc, carried on a frame made by cutting out the sides of a tea chest. A door, insulated with soil contained in a zinc frame, isolated this space, in which the humidity was 95 per cent., and the temperature only varied by 1°F. per diem. Details for the construction of more elaborate caves are given by McColloch (1917).

For the morphological study of external parts, larvae were fixed by immersion in boiling water, being transferred to 20 per cent. caustic potash for about two days, when they were ready for examination, either directly in water, or, after staining, in alcoholic carbol-fuchsin, followed by clearing in clove oil saturated with orange G. The latter showed well the comparative development of the chitinous structures.

External Morphology of the Mature Larva of Serica brunnea.

Although this larva has been described by Continental writers in general works on SCARABAEIDAE (Schiödte, 1874; Perris, 1875; Xambeu, 1903; Houlbert et Monnot, 1915), no English account of the functional morphology of a larva of this family exists.

Serica brunnea, L., belongs to the tribe SERICINI of the subfamily MELOLONTHINAE, of the family SCARABAEIDAE. The larva may be distinguished from those of other tribes by the separation of the malae of the maxillae, and by the longitudinal anal aperture. The latter character is said not to exist in the case of *Serica holosericea*, Scop. (Piochard de la Brûlerie, 1864), but it is figured by Böving & Craighead (1931) for *Aserica castanea*, Arrow, by Hayes (*l. c.*) for *Serica* sp., and seems to be well substantiated for the tribe as a whole.

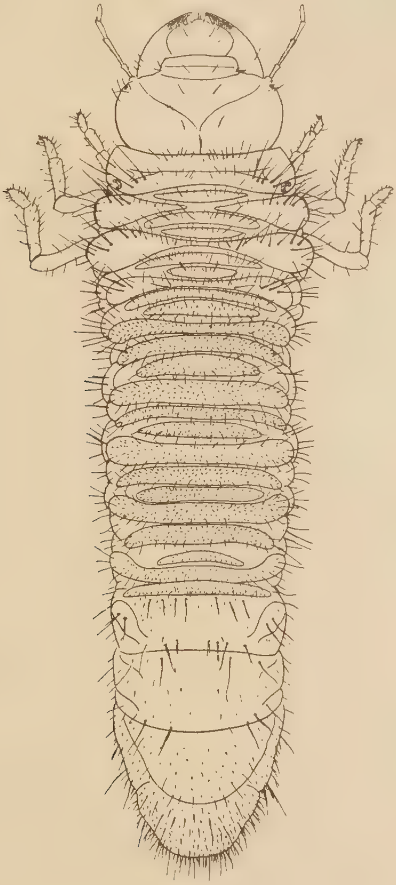

Fig. 1. *Serica brunnea*, L.: dorsal view of larva extended to show the chaetotaxy (× 6).

General Form.

This larva (fig. 1) conforms to the type well known as scarabaeiform, common to this group of the Coleoptera, whose immature stages spend their lives burrowing in either soil, dung, or rotten wood. When mature, it attains a length (extended) of 20–23 mm. It possesses a well developed chitinised head, with strong hypognathous mouthparts, adapted for biting and burrowing, and 13 body segments (12 according to

Perris), covered with a tough transparent setose cuticle, and furnished with three pairs of short legs, which are normally very little used for walking, since the body is strongly curved towards the posterior end whilst the larva is burrowing.

The Head.

Examining the head more closely, the *head-capsule* consists of a well marked epicranium and frons of a uniform light brown colour, and is a little wider at its widest part (just behind the ocellus) than long (fig. 2, A). The average head width of all stages of the larvae are given in Table II, with those of the two other common forest nursery pests, *M. melolontha*, L., and *P. horticola*, L., for purposes of comparison. In *S. brunnea*, the geometrical ratio between the stages is closely followed, in the other species the increase in size from larva II to larva III is smaller than this ratio would prescribe. The median suture (fig. 2) is very deeply marked along a short line on the vertex, and diverges anteriorly into two distinct lateral arms, which run forwards and outwards to end on the anterior margin, immediately in front of the antennifer. The chitin forming all the head sclerites shows a minutely reticulated structure. The epicranium is characterised by the sparseness of its setae, and by the presence of

TABLE II.

Maximum width of Epicranium.

Species	Egg	Larva I	Larva II	Larva III
Serica brunnea, L.	1·86 mm. × 1·37 mm.	1·18 mm.	1·86 mm.	2·77 mm.
Phyllopertha horticola, L.	2·03 mm. × 1·56 mm.	1·32 mm.	2·20 mm.	2·88 mm.
Melolontha melolontha, L.	3·0 mm. × 2·5 mm.	2·49 mm.	4·32 mm.	6·74 mm.

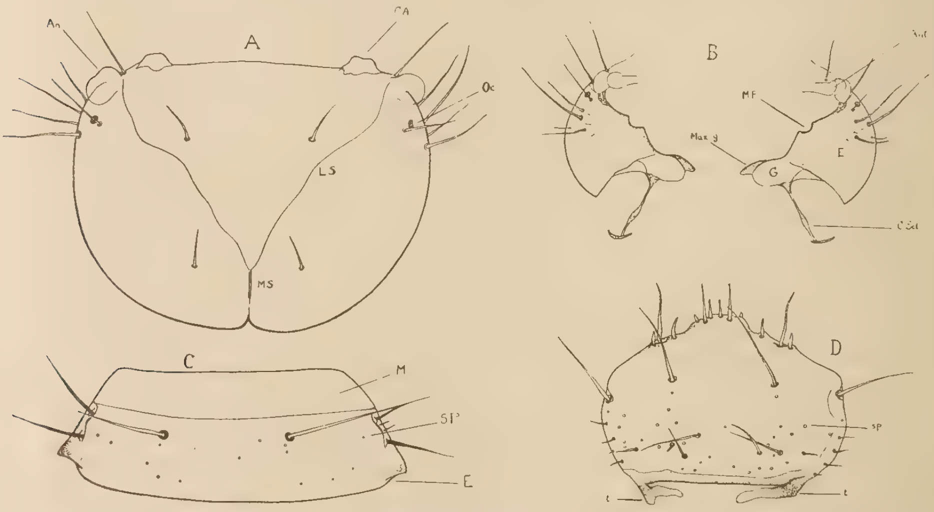

Fig. 2. *S. brunnea*, L. A, epicranium from above (× about 18) : *ms*, median suture ; *ls*, lateral suture ; *oc*, ocellus ; *an*, antennifer ; *ca*, clypeal articulation. B, epicranium from below (× about 18) : *e*, epicranium ; *g*, gula ; *ant*, antenna ; *mf*, mandibular facet ; *max. g*, maxillary ginglymus ; *c. scl*, cervical sclerites. C, clypeus (× about 20) : *m*, membranous area ; *sp*, sensory pores ; *e*, epicranial articulation. D, labrum (× about 20) : *sp*, sensory pore ; *t*, tormae.

a single ocellus on each side. There is only one pair of macrochaetae, planted in shallow depressions, one on each side of the point of intersection of the lateral sutures. The only remaining setae form a small group of sensory hairs, surrounding the ocellus.

The ocellus takes the form of a pigmented spot immediately behind the antennifer on each side of the epicranium. In early descriptions by Schiödte and Perris it is unmentioned, but Xambeu (1903) noted its presence and Böving & Craighead (1931) figure a similar structure in *Aserica castanea*, Arr. It is possibly a constant feature of the larvae of the SERICINI. In mature larvae about to pupate, its position moves higher on the epicranium, and the pupal eye can be seen forming beneath the cuticle. The ocellus is especially conspicuous in the two younger instars, and may be functional, since a few cases have been observed where larvae feed with the head-capsule visible, and even crawl on the soil surface at the base of grass stems.

The *frons* is triangular in shape, and bears two shallow foveae towards the apex in which macrochaetae are planted. The anterior corners are each furnished with a macrochaeta placed just in front of the antennifers. The absence of other setae on this sclerite distinguishes this larva from those of the other British chafers. The anterior margin of the frons is produced on each side into a conspicuous, heavily chitinised, condylar process, on which both the clypeus and the mandible are hinged.

Ventrally the *epicranium* is seen bending inwards from above (fig. 2, B), its front and back margins converging to a tongue-like plate, the gula, which is thickened apically, where the cardo of the maxilla articulates. Halfway along the anterior ventral margin of the epicranium there is a ginglymus for the articulation of the mandible, and at a point in the rear margin of the gula, the neck sclerites are attached. These consist of a narrow strut, strengthened longitudinally by heavier chitinization, carrying transversely, at its distal end, a small crescentic strut. These cervical sclerites are concerned with the muscles depressing the head.

The *clypeus* is subtrapezoidal in shape, two and a-quarter times as broad as long, and slightly convex transversely. It is clearly divided into a membranous anteclypeus, occupying the anterior third, and completely devoid of sensillae or setae, and well chitinized, a postclypeus bearing 6 macrochaetae (fig. 2, C), and a number of sensillae, all placed behind the line through the submedian macrochaetae.

The *labrum* (fig. 2, D) is one and a-third times as broad as long, slightly longer and narrower than the clypeus ; rounded at the sides and contracted at the base ; the sinuous front margin is produced into a median lobe. The surface is transversely convex and rugose, with a slight fovea on each side posteriorly and a deep fovea anteriorly. The dorsal macrochaetae vary slightly in number, usually there are 12 on each side, arranged as shown in the figure. The most important are the submedians, which appear to be serial with those on the clypeus, frons, and vertex.

The *epipharynx* is the membranous interior surface of the labrum. It bears a number of spines and setae, arranged in the asymmetrical fashion typical of nearly all Lamellicorn larvae (fig. 3, A). A comparative study of the features of the epipharynx is valuable in the separation of larvae of different species, and has been carried out by Hayes (1929) for American forms. Rittershaus (1927) described and named the parts of the epipharynx in *Phyllopertha horticola*, L., and *Anomala aenea*, de Geer. The terms of these two writers will be employed. The produced anterior area in *Serica* is thickly setose, most conspicuous being a strong transverse row, extending laterally from the apex and diminishing in size down the edges of the epipharynx. At the base of each of these lateral setae is a short inwardly directed ridge. These collectively form the lateral striae, typical of the MELOLONTHINAE.

The most prominent feature of the distal portion is an irregular chitinized area, bearing a number of sensory pores, and produced posteriorly into three very stout obliquely directed spines. This is known as the *distal sensory area*. Associated with this, on the membrane on each side, are a number of sense pores, to which reference will be made later. Between the distal sensory area and the hind margin of the membrane are numerous setae and spines of various sizes, mostly directed inwards towards a central non-setose area. Towards the proximal end of the epipharynx there are no articulate setae, and the cuticular spines converge towards a curious sensory organ, the *proximal sensory area* (Hayes, 1929). This consists of a chitinous plate, bearing a very stout tooth (fig. 3, *sc*) (Sinneskegel, Rittershaus, 1927), which is penetrated by four innervated campaniform organs, with their openings along the cusp of the tooth. There are two large sensory pores in the membrane on each side of the chitinous plate. The whole organ is placed at the entrance to the pharynx,

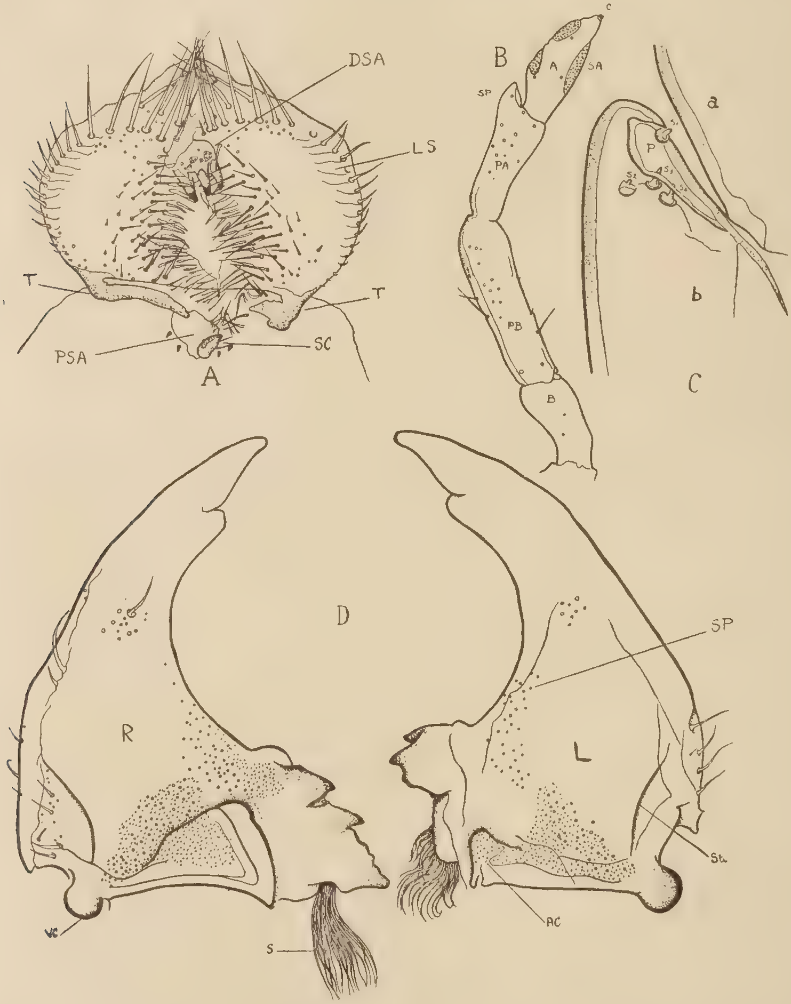

Fig. 3. *S. brunnea*, L. A, epipharynx of larva (× about 20): *ls*, lateral striae; *dsa*, distal sensory area; *psa*, proximal sensory area; *sc*, sense cone; *t*, tormae. B, antenna of larva: *b*, basal segment; *pb*, prebasal segment; *pa*, post-apical segment; *a*, apical segment; *c*, circlet of sensillae; *sa*, membranous sense areas; *sp*, sensory pit in process. C, sense organ in process of 3rd antennal segment: *a*, apical segment; *b*, process of 3rd segment; *p*, pit on inner face of process; *s*.1–*s*.4, sense pegs. D, ventral view of mandibles of larva: *l*, left mandible; *r*, right mandible; *vc*, ventral condyle; *ac*, accessory condyle; *s*, acia; *str*, stridulatory ridge; *sp*, sense pores.

and, from its specialisation, is evidently of considerable importance in the perception of the nature of the ingested material.

The tormae, or apodemes of the labrum, are important systematically and in *Serica brunnea* they are very asymmetrical, the narrow right arm extending halfway across the base of the labrum, the left being short and truncated. The labrum is moved very freely, the three stout oblique teeth assisting in working the food into the buccal cavity.

Antennae.

The antennae (fig. 3, B) are exceptionally well developed in mature larvae, attaining a length of 1·9 mm., or three-quarters of the width of the head. They are borne upon a basal process, or antennifer, and consist of the following segments :— Basal 0·4 mm., prebasal 0·7 mm., post-apical 0·4 mm. and 0·1 mm. process, and apical 0·4 mm. The post-apical segment is produced ventrally into a blunt process, membranous interiorly, and bearing four peg-like sensory organs. The apical segment tapers distally and ends in a circlet of minute papillae, which are supplied by the main nerve ; the surface of the segment is broken by three membranous areas studded with sense pores. The only setae present on the antenna are borne by the large prebasal segment.

Mandibles.

The mandibles are of the biting type, with the incisor and molar regions widely separated, the latter asymmetrical and complementary (fig. 3, D). The body of the mandibles is convex dorsally, tapering distally and then expanding into broad laminae, convex above and obliquely truncated at the apex, which is lanceolate. The posterior two-thirds of the body of the mandible are ferrugineous, the apical one-third black. The incisor blades have small, well-defined posterior lobes, marked off by curved dorsal sutures, with apices resembling those of the main blade, but shorter. These incisors have a two-fold function : by lateral action they sever the roots on which the larva feeds ; when placed together and acting vertically, they form an efficient shovel, which enables the larva to burrow into the soil with comparative rapidity (nine inches in one hour has been observed in *Melolontha melolontha*). The molars are asymmetrical and work in conjunction with the stout hypopharynx.

The *right molar* is tricuspidate, with a rounded tubercle anteriorly. The first, or posterior, cusp is large and backwardly directed ; it is bituberculate, and bears on its posterior margin a brush of long setae, the acia (fig. 3, D, *s*), which extends backwards into the pharynx and may assist the passage of the food into it. The second and third cusps are similar and smaller than the first, with longer, but simple inwardly directed crowns. The tubercle is borne on the front margin of the first cusp. Ventrally, the mandible articulates with the head-capsule by means of a stout hemispherical condyle, and interiorly to this, there is a large accessory condyle, which rocks in a facet on the side of the hypopharynx.

The *left molar* is hollowed, the double anterior cusp working on the rounded tubercle of the right molar, the hollow posterior portion receiving the cusps of this molar and also part of the hypopharyngeal tooth, which will be described later. The acia is shorter on the left mandible, but more widely distributed on the posterior margin of the molar. The accessory condyle is smaller by half than that on the right mandible. Both molars bear, in the region of the accessory condyles, a number of minute granulations, which are triangular denticles, visible only under high power magnification. These were supposed by Schiödte to be concerned in stridulation, but their presence in *Phyllopertha*, in which a striated area on the incisor exists for this function, tends to disprove the older hypothesis (see also Ohaus, 1899, Arrow, 1904). The denticles also occur on the other mouth-parts, and may possibly be concerned in maintaining a firm hold on the food. In *Serica*, the mandibular portion of the so-called stridulatory apparatus appears to be a curved ridge running obliquely from the ventral condyle to the outer margin (fig. 3, D, *str*). On this, the plectrum, or maxillary teeth, have been observed to grate, although no sound has been detected, even with a stethoscope applied to the cranium of the larva. The stridulating teeth of the maxilla certainly do not normally pass over the denticulated area on the mandibles. The inner ventral surfaces of the latter are well provided with sensory pores, which are constant in position (fig. 3, D, *sp*).

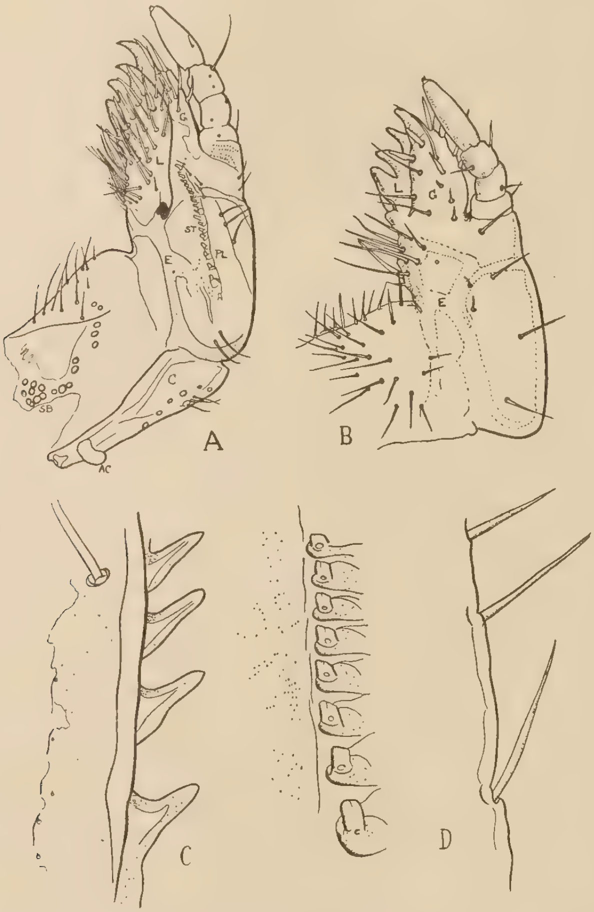

Fig. 4. *S. brunnea*, L. A, dorsal view of right maxilla of larva ; B, ventral view of left maxilla of larva : *c*, cardo ; *st*, stipes ; *g*, galea ; *l*, lacinia ; *ac*, articulating condyle ; *sb*, sensory button organs ; *pl*, plectrum of stridulating organ ; *e*, endoskeleton. C, teeth of the stridulating plectrum (from the side, very highly magnified). D, teeth of the stridulating plectrum (from above, basal portion of plectrum only, very highly magnified).

Maxillae.

The maxillae (fig. 4, A, B) are of the typical biting type, the chief feature being the separation of the malar lobes, which is probably a primitive feature in the group of the SERICINI.

The *cardo* is stout and consists of a well developed proximal and a slight distal sclerite ; the former bearing the condyle which articulates with the head-capsule. There are, upon these sclerites, and in the membrane of the cardo, curious chitinized button-like organs, which, in sections, appear to be innervated very highly. It is possible that these structures, which are also irregularly and more thinly distributed over the whole body of the larva, are used in the detection of sound or vibration, but no study of their function has been made.

The *stipes*, or body of the maxilla, when viewed from the side of the head, appears exceptionally broad and rounded and differs completely from the form shown by larvae of the other tribes. This outer surface tapers rapidly distally and bears scattered setae. Dorsally, on the body of the stipes and protected on its outer border by a setose chitinous ridge, runs a longitudinal row of stout truncate pegs, about 20 in number. This is the so-called plectrum of the stridulatory apparatus (fig. 4, C, D). The pegs appear to partake of the nature of articulate setae and tend to become conical anteriorly ; no transition to setae is, however, visible in mature larvae. The surface of the stipes, immediately interiorly to this row of pegs, is covered with minute granulations similar to those on the mandibles.

The stipital apodemes are found mainly on the ventral side, the folds which form them being visible externally as sutures. These apodemes serve as attachments for the powerful muscles which work the malar lobes.

The stipes bears a separate galea and lacinia, which are very deeply separated dorsally, but only to half of that extent ventrally. The galea is a broad fleshy setose lobe, some of the setae becoming stout or peg-like ; this lobe tapers distally and ends in a stout tooth or uncus. The lacinia, or internal lobe, resembles the galea, but is more heavily spinose and bears three stout unci.

The *maxillary palps* are well developed and are borne upon a well-defined basal area on the outer end of the stipes, the palpiger. This is more or less marked off by a suture from the basal palp segment, and is furnished with 5 transverse sinuous ridges bearing minute triangular denticles (fig. 4, A).

The palps themselves consist of 4 segments, which exhibit little movement *inter se.* They are composed as follows :—

Segt.	*Length (mm.)*	*Setae*	*Sensillae*
basal	0·1	—	1
prebasal ...	0·14	1 small	3
post-apical ...	0·16	2 stout	2
apical ...	0·3	1 ,,	2 + circlet of papillae

The length of the palp relative to that of the galea varies in different tribes of the MELOLONTHINAE. In *S. brunnea*, the apex of the galea reaches a point just short of the mid-point of the apical palp segment. The whole organ is capable of active movement, and serves to hold roots during their severance and later to work the particles into the buccal cavity. In active larvae the maxillae are always making quick intermittent stridulatory movements across the mandibular ridges (fig. 3, D, *str*).

Labium and Hypopharynx.

The *labium* consists of a basal plate or mentum, articulating with a broad fleshy setose lobe, the glossa, which bears at its distal end the short two-segmented palps. These sclerites give support to the muscles which work the floor of the buccal cavity and the important structure which is borne dorsally upon the labium—the *hypopharynx* (fig. 5, A, B). This is a strongly chitinized asymmetrical tooth, produced anteriorly on the right side into a cusp which works in conjunction with the right mandible, meeting it on its scissorial margin immediately above the anterior tuberculate tooth, and forming with it a cavity into which the anterior cusps of the left molar work. The hypopharynx bears on either side a chitinized facet, on which the accessory condyles of the mandibles (fig. 3, D) rock.

On its dorsal (buccal) face the hypopharynx bears, on the right side, two strong brushes of inwardly directed spines (fig. 5, A, *b*) which grade sharply in length from the anterior to the posterior margin of the tooth. On the left side, there is a broken sinuous line of similar spines, borne upon the more posterior membranous part of the hypopharynx (*h. sp.*). The most anterior of these are homologous in position and structure with those of *Phyllopertha horticola*, in which they are stated by Carpenter & McDowell (1912) to be vestiges of maxillulae. No evidence of an appendicular origin can be seen in *Serica brunnea* ; the spines are not articulate setae, and every gradation in size can be found, down to the minute triangular denticles which cover the unchitinized part of the hypopharynx and the membrane of the pharynx itself. These setose brushes are probably concerned in working the food material from the molar cavities into the pharynx. The relation of the pharynx to its upper and lower bounding structures is seen in fig. 5, B.

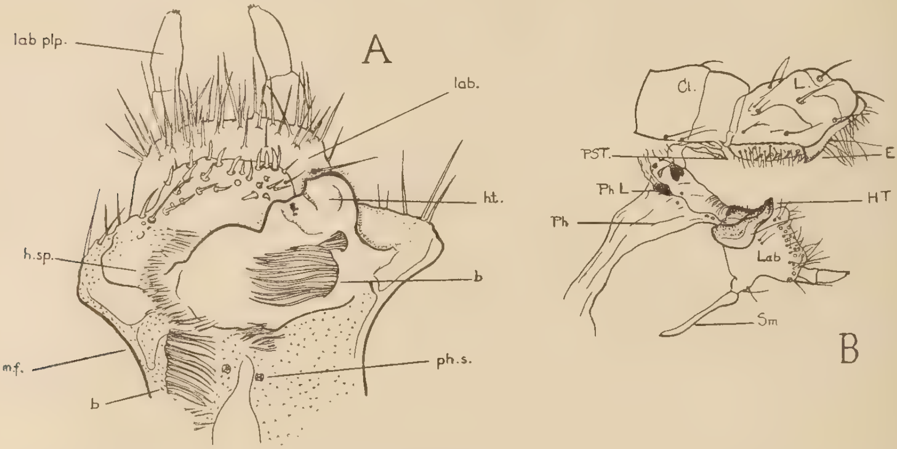

Fig. 5. *S. brunnea*, L. A, labium and hypopharynx of larva, dorsal aspect : *lab*, labium ; *lab. plp*, palp ; *ht*, hypopharyngeal tooth ; *ph. s*, sense-organ of pharynx ; *hsp*, hypopharyngeal spines ; *b, b*, brushes of spines ; *mf*, mandibular articulating facet. B, buccal cavity of larva (mandibles and maxilla removed) : *l*, labrum ; *cl*, clypeus ; *lab*, labium ; *et*, epipharyngeal tooth ; *ht*, hypopharyngeal tooth ; *sm*, mentum ; *pst*, tooth of proximal sensory area ; *ph*, pharynx ; *ph. l*, pharyngeal ligament.

The Thorax (fig. 1).

Viewed dorsally, the thoracic region of the larva is well distinguished from that of the abdomen on account of its markedly greater width. The metathorax is slightly longer and broader than the mesothorax, giving to the larva a characteristic shape which renders it easy to distinguish at a glance from other chafer larvae. The dorsal folds or annulations of the thorax are not so well marked as those of the abdominal segments, which provide attachment for muscles producing the strong contractile body movements.

The prothorax is specially modified in connection with the muscles which move the head. The legs of this segment are the most weakly developed pair. Dorsally the segment is divided into two annulets by a weak suture, which becomes a deep furrow laterally. The triangular area in front of this furrow is thickened so as to provide skeletal strength for the attachment of the depressors of the head. The area is not pigmented as in *Rhizotrogus* and *Melolontha*. The pleuron extends forward so as to overlap the epicranium slightly. It is only weakly expanded into lobes, laterally, and bears on its posterior margin the prothoracic spiracle.

The meso- and metathorax are tri-annulate, the first and third annuli being keel-shaped pads, overlapping and almost crushing out the second annulus dorsally, but tapering rapidly and disappearing laterally. The lateral lobes of the second annulus are strongly developed in relation to the legs, which are remarkably prominent in this group of soil-inhabiting larvae. Only the fore legs, which are shorter and more closely set together than the other two pairs and which are sometimes used to manipulate the food of the larvae, are in any way reduced. The structure of all three pairs of legs is similar (fig. 6, B) ; the coxae are stout and cylindrical and bear a few long setae. There is a proximal projection for the articulation with the pleural lobes. The femora are slightly shorter than the coxae and show some indications of the presence of a trochanter, especially in the long metathoracic legs. The femoral apodeme at the coxal articulation is specially prominent. The tibiotarsi are short and stout, those of the pro- and mesothoracic legs bearing many stout setae. This segment tapers but slightly distally and ends in all three pairs of legs in a short stout claw (*cf.* the claws of Melolonthini, in which the metathoracic claw is greatly reduced, and those of Rutelini, in which all three claws are equally long and thin).

The thorax and the femora of the metathoracic legs only bear a few of the button-like organs similar to those found in the cardo of the maxillae (fig. 6, B, *sb*).

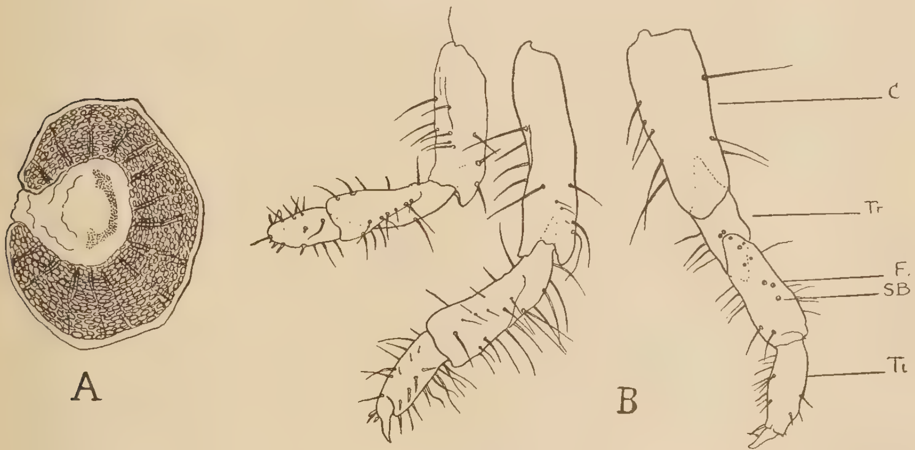

Fig. 6. *S. brunnea*, L. A, first abdominal spiracle of larva. B, legs of larva seen from the side (N.B. sense-buttons only on third pair) : *c.* coxa ; *tr*, trochanter ; *f.* femur ; *t*, tibio-tarsus ; *sb*, sense-buttons.

The Abdomen.

The abdomen (fig. 1) is divided into three regions. The first segment, viewed dorsally, forms a region transitional from thorax to abdomen, the first two annuli resembling those of the former region, whilst the third shares all the characters of an abdominal annulus. The second region, comprising abdominal segments 2–6, constitutes the chief locomotory organ of the larva. Here, the three annuli of each segment are more equally developed dorsally into broad muscular pads covered with spinules, the crawling pads (Kreichwülste of Rittershaus, 1927). Laterally the mesotergite, as in the thorax, expands into a prominent lobe, and at its pleural extremity, divided from it by a suture, is a crescentic lobe, expanded anteriorly, where it bears the spiracle. The homologies of the pleural region of larval Scarabaeidae have been discussed by Böving & Craighead (1931).

Segments 7–10 constitute the region known as the sac (Erichson). Annulation has disappeared but for traces laterally, near the stigmatic lobes. The cuticle is here very thin, and the internal organs, most prominently the colon with its brown contents, are visible through it.

Segment 9, which Perris (1875) considers to be the terminal segment, bears a dorsoventrally flattened lobe laterally, which projects slightly, and is separated from segment 10 only by a weak dorsal suture. The latter segment tapers to a blunt extremity where the anus is placed.

Ventrally, the abdomen is simply segmented, but the anal segment (9+10) bears the systematically important *radula* or *raster* (fig. 7). This consists of a group of stout spinules, arranged in a characteristic fashion ; their function seems to be that of cleansing the head and mouth-parts of soil particles. In *Serica brunnea*, the anal aperture is longitudinal (in the other tribes of the subfamily, this aperture runs transversely) and is densely surrounded by setae ; just above its ventral extremity runs a symmetrically disposed transverse arc of short stout spinules. This character, although it serves to distinguish *Serica brunnea* immediately amongst the British chafers is very uniform throughout the genus *Serica* (*sens. lat.*), within which it is of little systematic value.

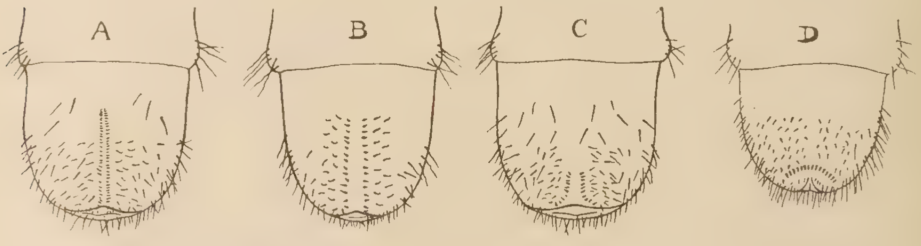

Fig. 7. Characteristic setal pattern of the radula (raster) of four British chafer larvae : A, *Melolontha melolontha*, L. ; B. *Phyllopertha horticola*, L. ; C, *Rhizotrogus solstitialis*, L. ; D, *Serica brunnea*, L.

The narrowest part of the abdomen is between the fifth and sixth segments, and this part of the body is normally kept curved beneath the thorax like a letter C, though the Sericini, in common with the Rutelinae and Dynastinae, can walk along smooth surfaces with the abdomen straightened and dragging behind them.

Spiracles.

The structure of all the spiracles is similar ; that of the thorax is larger than the others, and the crescentic sieve-plate area is more extensive, the tips of the crescent being directed posteriorly. The latter position is reversed in the case of the abdominal spiracles.

The perforations of the sieve-plates are disposed quite irregularly, the sizes of the holes being also irregular (fig. 6, A). The sieve-plate is supported by a number of radial thickenings, the trabeculae. In the bulla, which is irregularly thickened, no trace could be found of the slit figured by Imms (1925, p. 109) as the true spiracular opening. There is no evidence to show that the sieve pores are not the true respiratory apertures.

There are nine pairs of spiracles present, one placed on the hind border of the prothorax and eight abdominal pairs borne on stigmatic lobes extending forward from the lateral extremities of the mesotergites. These lobes are much reduced on segments 7 and 8 (" sac " segments).

Chaetotaxy of the Body.

The body of the larva of *Serica brunnea* is more densely covered with brown hairs than those of chafers belonging to the other tribes, the dorsal abdominal spinules particularly being more extensive and abundant.

In the thoracic region, there is a dorso-lateral group of prominent setae on each meso-tergite, which feature extends to the first abdominal segment. There are a number of small setae on each annulus (fig. 1). The dorsal annuli of the abdominal segments 2–6 are thickly armoured with short stout articulate setae (spinules), interspersed with small clothing hairs. Laterally, each of the pleural lobes bears a group of long setae. The delicate membrane of segments 7–10 bears several long hairs dorso-laterally, the setae becoming very dense on the anal segment, the arrangement ventrally being characteristic (fig. 7). Ventrally the setae consist of a single transverse line of fairly long hairs on each sternite.

Sense Organs.

Apart from the ocelli, whose function would appear of limited use, the larva of *Serica brunnea* is richly furnished with structures for the perception of conditions existing in its environment, such as touch, smell, taste and vibration, though the degree of differentiation of these senses is obviously limited.

Innervated articulate setae occur all over the body, and in no definite arrangement, being externally in no way distinct from ordinary clothing hairs. They grade in size from minute points visible only under high power, to the long bristles on the side of the head, grouped round the ocellus. The nerve connections are made visible by *intra vitam* staining with methylene blue, which is injected in 0·75 per cent. aqueous solution into the body cavity of the larva. Examination is then made by mounting small portions of the stained tissue in glycerine jelly.

The second type of sense-organ is the innervated pit, visible externally as a minute bordered pore ; they are found chiefly on the head and mouth-parts, in some cases being grouped together to form a definite organ. Single pores are found scattered over the epicranium but are densest in the region round the ocelli and again in the gular area. There are about 33 pores on the labrum and only 15 on the clypeus, quite irregularly placed (fig. 2, C, *sp*). The antennae (fig. 3, B), in addition to about 50 pores scattered along their length, each have 3 extensive membranous pits on the apical segment. The surface of these pits is thickly supplied with simple pores. Analogous structures in *Cotinis nitida* (Ceton.), the green June beetle of the U.S.A., are figured by McIndoo (1931, p. 51). On the mandibles, pores occur only on the ventral face, and their distribution is curious (fig. 3, D, *sp*). On the left there are just over 70 and on the right more than 110 arranged in a belt running from the region of the dorsal condyle to the anterior malar region. The maxillae are devoid of pores, except for a few on the palp ; the labium also bears no true pores, but on both appendages there are many minute sunken hairs with nerve connections, which at first sight would be taken for pores. These distinct structures are found also on the epipharynx.

The legs and thorax bear scattered pores, but there are none on the abdomen. There seems little doubt that these organs serve to receive chemical stimuli either from a distance, as in the case of the antennae, or from food which is being handled by the mouth-parts. A third type of innervated structure, characteristic of the larvae of Sericini, but not observed in larvae of the other tribes, is a chitinized disc with a distinctly thickened border. These discs are thick and are attached below to a dense layer of nervous tissue, which is itself richly supplied with sensory nerve connections. These have been seen in sectioned material stained with Delafield's haematoxylin. The distribution of these groups of discs is limited. They occur most thickly on the ventral and anterior faces of the maxillary cardo, but on no other portion of the head or mouth-parts. On the body, they are very diffusely distributed, but are most conspicuous on the pleural region of the thorax, and in the thoracic intersegmental membrane. A few discs also appear on the femora of the metathoracic legs (fig. 6.) Their function is unknown, but it seems possible that they may be concerned with the perception of the stridulatory vibrations made by the larvae.

The remaining sensory structures may be briefly tabulated as follows :

1. Groups of 6 or 7 papillae forming a circlet at the tips of the antennae, and of the maxillary and labial palps (figs. 3, B ; 4, A ; 5, A). These are strongly innervated by the main nerve which runs into each of these appendages. They are adapted for receiving delicate touch stimuli, but are said by McIndoo (*l.c.*) to be olfactory organs.

2. A cavity in the inner face of the process borne by the post-apical antennal segment bears four minute but stoutly built chitinous pegs, which project into it (fig. 3, C). These pegs are innervated from a branch of the antennal nerve, but the function of the whole organ is unknown.

3. The epipharyngeal sensory areas have already been described in connection with the morphology of the epipharynx itself.

4. The hypopharynx and the part of the pharynx immediately behind it bear, in the membrane, a few curious sense-organs consisting of a short thick peg sunk in a pit, the whole being raised from the surface giving the peg the appearance of being surrounded by a collar. There is a pair of these pegs just behind the hypopharyngeal spine brushes (fig. 5, A, *ph.s*) and two groups of three below the insertion of the pharyngeal ligament. The function of such pegs is unknown.

The histology of these sensory structures was not studied in any detail, since it conforms closely to the well known types. It remains for future work to explain adequately the functions of the various organs described.

Internal Anatomy.

A general study of the internal anatomy of the larva was made, both by dissection and by sectioning. In the latter method, very fair series of sections, even of the head, were obtained by paying special attention to the wax impregnation of the whole larva, which was first cleared in cedar oil, and then removed to the chloroform wax mixture. The sections were cut at 4μ–6μ with a Cambridge Rocker microtome and stained in Delafield haematoxylin.

The respiratory, muscular and circulatory systems were not studied in detail ; but the digestive and central nervous systems, which offer conspicuous characters for the identification of the larvae, will be considered here. The disposition of these systems within the body of the larva is shown diagrammatically in fig. 8.

Alimentary Canal.

The *pharynx* narrows into a short oesophagus, which expands into a more or less distended thin-walled sac, the *crop*. This consists of a layer of epithelial cells supported by a basement membrane and furnished with two layers of weak muscles, longitudinal and circular. A continuous peristalsis of this organ is observed, passing from front to rear. The chitinous intima was not successfully demonstrated and no evidence was found of secretory cells or pores, which Wiedermann (1930) suggests may fulfil the function of the missing salivary glands. Nevertheless, the contents of the crop are almost always very fluid, of a dark colour, and on irritation, the larva will disgorge acrid, dark brown drops. It thus appears that the first processes of digestion take place in the crop.

The crop passes, by a very distinct invagination, into the *midgut*, which has a more robust appearance, due to the possession of a thicker muscular layer. The lining epithelium consists of large cells, many of which are vacuolated and appear to be concerned in the passage of fluid either to or from the gut. There are certain highly characteristic diverticula of the midgut ; anteriorly there are eight rounded pouches, whose lining is the same as that of the midgut. The median diverticula are very small in this species, appearing as biramous outgrowths of the midgut, the arms pointing backwards and forwards. There are 21 of these diverticula, which in sections show a structure identical with that of the rest of the midgut, and their lumen narrows rapidly at their junction with it. There are no true posterior diverticula as found in DYNASTINAE.

The midgut tapers slightly posteriorly, and at its junction with the wider ileum, the four malpighian tubules are attached. The course of the tubules of one side are shown in fig. 8. This feature is interesting in view of the work of Edwards (1931) who found that, in the larva of *Dorcus parallelopipedus*, L., the two tubules of each side were continuous at their extremities. In *Serica*, after the initial divergence, the tubules run together beside the ileum, turn dorsally, and follow a tortuous course on the ventral face of the colon ; on joining again, they run together into the fat-body round the anus, and there they end independently in two closely adpressed bulbs. It was only after repeated dissections that it was established that actual coalescence did not take place.

The *small intestine* is short and tapers rapidly to its union with the *colon*. This important structure, which plays a large part in absorption of food materials, is a very thin-walled sac, bilobate posteriorly, and dorso-ventrally twisted back upon itself, a condition which increases its absorbing surface. In sections, the colon is seen to possess finger-like invaginations over its entire surface, which bear internal arboriform outgrowths, and are known as the arboriform processes (Wiedermann, 1930). These processes evidently enable the body fluids to come into intimate association with absorbable food material, and it is highly probable that an osmotic diffusion of nutrients takes place. No trace was found of areolar areas between the arboriform processes which, according to Mingazzini (1889), perform the function of absorption.

The waste products of digestion pass into the rectum at the anterior ventral end of the colon. The rectum, which is thin-walled and possesses but weak musculature, turns ventrally and runs straight back, expanding into a wide rectal sac, with scarcely a trace of constriction. In the first-stage larva, there is a circlet of backwardly directed spines projecting into the lumen of the rectum ; but there is no trace of this structure in mature larvae. The faeces, which are formed in the rectum, are, in larvae such as that of *Serica brunnea* which feed on succulent tissue, fairly liquid, in contrast to the dry pellets of certain RUTELINI and the subfamily DYNASTINAE, which feed on plant detritus. The hind intestine does not appear to function as an extractor of ingested and secreted liquid, so as to preserve the water balance in the body, as it does in the case of many larvae having a sub-aerial existence.

In the contents of the mid-intestine there have been found many ciliates and fewer flagellates, which are probably commensals, feeding on the bacteria always present in the gut. Records of symbiotic digestion in this group are confined to Werner's (1926) contention that *Bacterium cellulosum* plays an essential rôle in the nutrition of the inquiline larva of *Cetonia floricola*, Hbst. Further work to discover whether an obligatory symbiosis exists in the case of root-feeding chafer larvae is urgently needed.

Central Nervous System (fig. 8).

The nerve ganglia exhibit a considerable degree of concentration and fusion. There is a pair of well-developed, partly fused, cerebral ganglia linked by slender para-oesophageal connectives to the suboesophageal ganglion, which lies in the posterior part of the head and is closely connected by distinct though short connectives with the large first thoracic ganglion. The second and third ganglia are similarly connected, the former being the smallest and the latter the largest of the oval thoracic ganglia. The first abdominal ganglion is fused deeply to the posterior part of the third thoracic ganglion. The remaining seven ganglia are closely fused, but retain evidence of their double origin, especially in the case of ganglia 4–8. The last ganglion consists of the fused ganglia of segments 8, 9 and probably 10 ; there is a distinct furrow between the two first named. All the ganglia are contained in the first three thoracic segments of the larva.

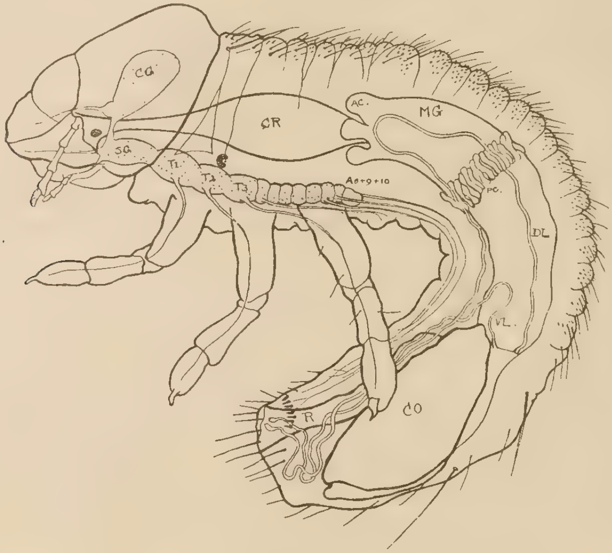

Fig. 8. *S. brunnea*, L., arrangement of the internal organs of the larva (diagrammatic) : *cr*, crop ; *mg*, mid-gut ; *dl*, dorso-lateral, and *vl*, ventro-lateral, malpighian tubules ; note the terminations ; *co*, colon ; *r*, rectum ; *ac*, anterior caeca ; *pc*, posterior caeca ; *cg*, cerebral ganglion ; *sg*, suboesophageal ganglion ; *t* 1, 2, 3, thoracic ganglia ; *a*8+9+10, last abdominal ganglion.

The cerebral lobes serve the antennae, ocelli, clypeus and labrum ; the suboesophageal ganglion gives branches to all the mouth-parts, and lateral nerves from each ganglion run back to their respective body segments.

A well developed frontal sympathetic ganglion is present, giving off a nerve which runs along the dorsal side of the alimentary canal. No hypocerebral ganglia were found, either by dissection or in longitudinal sections.

Fat-Body.

The presence of abundant fat-body in larvae of *Serica brunnea* is evidence either of approaching hibernation or of maturity. At these times the larva loses its delicate membranous appearance, becoming uniformly cream-coloured and almost waxy. In feeding larvae, the visceral fat-body appears typically on the dorsum of the colon as two lung-shaped sheets, visible through the membranous cuticle.

General Remarks.

Internal changes in structure during larval development are few, and concern only the number and development of the caeca of the midgut. In mature larvae, two rosette-like structures appear attached ventrally in the region of the colon. These are divided into six lobes and are the rudiments of the adult gonads.

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COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st September and 31st December, 1936.

Agricultural Research Service, Khartoum :—4 Diptera and 20 tubes of Coccidae ; from the Sudan.

Mr. P. N. Krishna Ayyar :—15 Coleoptera and 45 Parasitic Hymenoptera ; from South India.

Dr. T. V. Ramakrishna Ayyar :—7 Parasitic Hymenoptera and 4 cocoons, and 10 Lepidoptera ; from South India.

Mr. C. J. Banks :—7 Parasitic Hymenoptera and 14 cocoons ; from England.

Bernice P. Bishop Museum, Honolulu :—519 Curculionidae ; from Melanesia.

Dr. F. S. Bodenheimer :—7 Coleoptera ; from Palestine.

Dr. G. Bondar :—221 Coleoptera, 4 Tenthredinidae, and 2 Blattidae ; from Brazil.

Mr. H. E. Box :—13 Culicidae, 46 other Diptera and 17 pupa-cases, 400 Curculionidae and 400 early stages, and 725 *Diatraea* early stages ; from the West Indies.

Messrs. P. R. Buchanan & Co. :—4 Coleopterous larvae ; from England.

Mr. B. D. Burks :—6 Parasitic Hymenoptera ; from U.S. America.

Mr. P. J. Burton :—45 Parasitic Hymenoptera ; from England.

Prof. P. A. Buxton, London School of Tropical Medicine :—4 Tabanidae ; from Tanganyika Territory.

Chief Entomologist, Pretoria :—6 Curculionidae and 3 early stages, 110 Parasitic Hymenoptera, and 8 Lasiocampid cocoons ; from South Africa.

Mr. A. F. Clark :—17 Coleoptera ; from New Zealand.

Father P. A. Conrads :—35 Coleoptera ; from Tanganyika Territory.

Coryndon Memorial Museum, Nairobi :—108 Diptera and 10 Parasitic Hymenoptera ; from East Africa.

Mr. A. Cuthbertson, Entomologist :—20 Coleoptera, 6 Parasitic Hymenoptera, and 2 Lepidoptera ; from Southern Rhodesia.

Dr. A. da Costa Lima :—30 Coleoptera ; from Brazil.

Mr. R. C. M. Darling :—19 Culicidae, 5 other Diptera, 246 Coleoptera, 3 Hymenoptera, 93 Lepidoptera, 34 Rhynchota, 286 Orthoptera, 15 Planipennia, and 50 Mites ; from Arabia.

Mr. H. J. de Kerville :—3 Parasitic Hymenoptera ; from France.

Mr. M. Delassus :—8 Parasitic Hymenoptera ; from Algeria.

Director of Agriculture, Fiji :—2 Coleoptera and 3 early stages.

Director of Agriculture, British North Borneo :—17 Coleoptera.

Director of Agriculture, Zanzibar :—25 Coleoptera.

Director of Locust Research, Pretoria :—2 Coleoptera and 79 Orthoptera ; from South Africa.

Director of Veterinary Services, Gold Coast :—31 Coleoptera.

Mr. H. L. Dolton :—A collection of *Apanteles* cocoons ; from England.

Mr. R. G. Fennah :—1 Sphegid and 1 Gryllotalpid ; from the British West Indies.

Mr. J. C. M. Gardner, Systematic Entomologist :—35 Diptera and 20 pupa-cases, and 35 Parasitic Hymenoptera ; from Burma.

Mr. F. D. Golding, Government Entomologist :—4 Culicidae, 45 *Glossina*, 35 other Diptera, 58 Coleoptera, 3 Parasitic Hymenoptera, 2 other Hymenoptera, 32 Lepidoptera, 35 Rhynchota, and 149 Orthoptera ; from Nigeria.

Government Entomologist, Coimbatore :—28 Diptera, 4 Coleoptera, 16 Lepidoptera, 1 species of Coccidae, and 7 other Rhynchota ; from South India.

Government Entomologist, Lyallpur :—1 species of Coccidae ; from the Punjab.

Government Entomologist, Mandalay :—15 Rhynchota ; from Burma.

Mr. W. B. Gurney, Government Entomologist :—5 Lepidoptera and 16 Orthoptera ; from New Zealand.

Mr. E. J. Hambleton :—41 Curculionidae ; from Brazil.

Mr. G. L. Hey :—2 Parasitic Hymenoptera ; from England.

Mr. E. Hargreaves, Government Entomologist :—77 Diptera, 184 Coleoptera, 7,010 Parasitic Hymenoptera, 17 other Hymenoptera, 79 Lepidoptera, 40 Rhynchota, 4 Orthoptera, 4 Hemimeridae, 9 Planipennia, 10 Thysanura, and 1,000 Mites ; from Sierra Leone.

Mr. H. Hargreaves, Government Entomologist :—79 Diptera, 207 Coleoptera, 18 Parasitic Hymenoptera, 7 other Hymenoptera, 398 Lepidoptera, 400 Thysanoptera, 13 species of Aphidae, 3 species of Psyllidae, 58 other Rhynchota, 50 Psocidae, 11 Orthoptera, and 150 Mites ; from Uganda.

Mr. W. V. Harris, Entomologist :—8 Diptera, 4 Lepidoptera, 100 Thysanoptera, 1 species of Coccidae, and 8 other Rhynchota ; from Tanganyika Territory.

Mr. G. H. E. Hopkins, Entomologist :—35 Hemimeridae, 550 Anoplura, 60 Ticks, and 60 Mites ; from Uganda.

Imperial Chemical Industries, Ltd. :—30 Diptera and 16 Mites ; from England.

Inspecteur de la Defense des Cultures, Algeria :—6 Parasitic Hymenoptera and 4 Lepidoptera.

Institute for Plant Diseases, Buitenzorg :—192 Coleoptera and 2 Lepidoptera : from the Netherlands Indies.

Dr. C. A. Isaakides, Government Entomologist :—22 Parasitic Hymenoptera ; from Greece.

Mr. C. B. R. King :—20 Mites ; from Ceylon.

Mr. L. A. L. King :—5 Diptera and 5 pupa-cases, and 2 Parasitic Hymenoptera ; from Scotland.

Mr. T. W. Kirkpatrick, Entomologist :—4 Rhynchota ; from Tanganyika Territory.

Dr. W. A. Lamborn, Medical Entomologist :—2 Culicidae, 10 Tabanidae and 12 early stages, 9 other Diptera infested by Mites, and 10,000 Formicidae ; from Nyasaland.

Mr. A. W. Lazaroff :—11 Parasitic Hymenoptera ; from Bulgaria.

Dr. R. H. Le Pelley :—110 Parasitic Hymenoptera ; from the Philippine Islands.

Mr. R. A. Lever, Government Entomologist :—6 Culicidae, 43 other Diptera, 88 Coleoptera, 100 Formicidae, 30 Lepidoptera, 500 Isoptera, 1 species of Coccidae, 1 species of Aphidae, 3 other Rhynchota, 2 Psocidae, 100 Mites, 5 Millipedes, and 20 Crustacea ; from the Solomon Islands.

Mr. C. J. Louwerens :—34 Coleoptera ; from Java.

Prof. P. Maréchal :—33 Parasitic Hymenoptera ; from Belgium.

Mr. U. Bahadur Mathur :—19 Diptera, 6 Parasitic Hymenoptera, and 4 Orthoptera ; from the Punjab.

Prof. F. J. Meggitt :—15 Coleoptera ; from Burma.

Mr. H. M. Morris, Government Entomologist :—1 species of Coccidae ; from Cyprus.

Dr. C. F. W. Muesebeck :—42 Parasitic Hymenoptera ; from various localities.

Mr. J. Muggeridge, Government Entomologist :—9 Parasitic Hymenoptera, 1 species of Coccidae, and 1 species of Eriophyidae ; from New Zealand.

Musée du Congo Belge :—40 Coleoptera and 4 Parasitic Hymenoptera ; from the Belgian Congo.

Mr. F. B. Notley, Entomologist :—2 Coleoptera ; from Tanganyika Territory.

Mr. J. Palmoni :—243 Coleoptera, 97 Formicidae, 51 Lepidoptera, 25 Orthoptera, 5 Embiidae, 13 Planipennia, 19 Odonata, 24 Trichoptera, 5 Thysanura, and 4 Wood-lice ; from Palestine.

Mr. E. F. Peck, Veterinary and Agricultural Officer :—4 Lepidoptera, 1 species of Aphidae, 5 other Rhynchota, 223 Orthoptera, and 2,020 Ticks ; from British Somaliland.

Mr. R. Pussard :—80 Parasitic Hymenoptera ; from France.

Mr. Y. R. Rao :—4 Orthoptera and 1 species of Mite ; from Karachi, India.

Dr. P. Regnier :—9 Parasitic Hymenoptera ; from Morocco.

Dr. O. W. Richards :—288 Parasitic Hymenoptera and 350 cocoons ; from England.

Mr. P. A. Robert :—3 Parasitic Hymenoptera ; from Switzerland.

Dr. K. E. Schedl :—480 Parasitic Hymenoptera ; from Germany.

Selangor Museum :—2 Diptera, 177 Coleoptera, and 30 Parasitic Hymenoptera; from Malaya.

Mr. C. Smee, Government Entomologist :—100 Thysanoptera ; from Nyasaland.

Dr. C. Strickland :—22 Parasitic Hymenoptera ; from Calcutta, India.

Mr. K. Subrahmanian :—4 Diptera, 86 Coleoptera, 8 Hymenoptera, 25 Rhynchota, and 14 Orthoptera ; from Burma.

Dr. P. Tchorbadjiev :—4 Coleoptera ; from Bulgaria.

Mr. A. Théry :—93 Coleoptera ; from various localities.

Dr. O. Watzl :—3 Parasitic Hymenoptera ; from Austria.

West Java Experiment Station :—5 Coleoptera, 20 Lepidoptera, and 3 Rhynchota ; from Java.

Mr. F. G. S. Whitfield, Medical Entomologist :—18 Culicidae, 2 Tabanidae, 298 other Diptera, 6 Coleoptera, 2 Hymenoptera, 8 Lepidoptera, 5 Rhynchota, 3 Orthoptera, and 3 Ephemeridae ; from the Sudan.

Mr. F. Wilson :—15 Diptera, 2 Lepidoptera, and 1 species of Aphidae ; from France.

Mr. E. C. Zimmerman :—3 Curculionidae ; from Fiji and Samoa.

Zoological Museum, Copenhagen :—900 Parasitic Hymenoptera ; from Denmark.

Dr. F. Zumpt :—637 Coleoptera ; from the Cameroons.

ON A NEW SPECIES OF ECHTHROMORPHA (HYM. ICHN.) FROM FIJI.

By J. F. Perkins, B.Sc.
Department of Entomology, British Museum.

Echthromorpha tirathabae, sp. n.

This species belongs to Group D of Krieger's monograph of this genus (Mitt. zool. Mus. Berlin, **4,** 1909, p. 341).

♀. Head and antennae testaceous; prothorax testaceous, black laterally, with the presternum infuscate; mesonotum, tegulae, scutellum, post-scutellum and propodeon dorsally testaceous; meso- and meta-pleura and sterna black; legs testaceous, with the front coxae marked with black posteriorly, and the middle (usually entirely) and hind coxae black, the middle trochanters black (or black marked), and the hind trochanters and femora (except for the extreme base and apex) black; abdomen with the first tergite testaceous, the second to fourth black and the remainder testaceous; the ovipositor sheaths black. Wings light smoky yellow, the stigma testaceous strongly margined with black, the veins black.

Head: Frons strongly excavate, with a very shallow longitudinal central groove before the anterior ocellus, very weakly (hardly visibly) trans-striate above the antennal scrobes; face quadrate and strongly shining, with few scattered punctures beneath the antennal scrobes; clypeus as long as broad, very weakly divided from the face, apically truncate and smooth; the cheeks twice as long as the breadth of the base of the mandibles, with short pubescence; flagellum with 33 to 35 segments, the 1st flagellar joint 7 times as long as its breadth in the middle. *Thorax*: Pronotum with the epomiae present, the hind angles finely punctured and below this with short coarse striae before the hind margin, centrally with a faint indication of irregular striae below the epomiae; presternum dull, very finely and closely punctured; mesonotum closely coarsely punctured; mesopleura smooth and shining with only very few scattered punctures towards the anterior margin, somewhat raised towards the dorsum (below the callus) and with a distinct tubercle before the base of the middle coxae; mesosternum sparsely punctured; epicnemia abbreviated above; mesopectus sparsely punctured below, more closely punctured above; scutellum smooth, prominent and not keeled laterally; post-scutellum smooth; propodeon with a pair of strong tubercles towards the apex, centrally and laterally trans-striate, rugose-punctate dorsally at the sides and apically smooth; metapleurae smooth, only weakly sculptured apically. *Legs*: Fore coxae finely punctured internally, middle coxae finely punctured at the base and the hind coxae sparsely shallowly punctured (but more distinctly at the base). *Abdomen*: 1st tergite weakly channelled centrally; almost without punctures; ovipositor sheaths as long as the hind tarsi.

Length: 13 mm.; ovipositor, 4 mm.

♂. Differs from the female in having the clypeus, cheeks and orbits (except on the vertex) yellow; the area between the ocelli black; the pleura and sterna testaceous, weakly marked with yellow; the coxae and trochanters testaceous, except for the hind coxae which are infuscate; the hind tibiae black apically, and the hind tarsi black; the scutellum less strongly raised; the mesopleura more strongly punctured; the face distinctly longer than broad and the coxae unsculptured. Length, 7 mm.

Fiji: Taveuni, ♀ iii.1934 (*type*), ♂ i.1934 (*allotype*) (bred in captivity from unmated ♀), 1 ♀ xii.1933, 1 ♀ ii.1934, 1 ♂, 4 ♀♀ viii.1934 (*R. W. Paine*); 1 ♂, 2 ♀♀ 1929 (*T. H. C. Taylor*).

Type deposited in the British Museum.

Host: This species is stated to have been bred from *Tirathaba trichogramma*, Meyr., a pest of coconuts.

The known species nearest to *E. tirathabae* is *E. ceramocare*, Vach. (=*bitecta*, Morl). Besides differing very markedly from this species in colour, it differs also in the following structural and sculptural characters :—Frons with a weak median groove ; face less strongly grooved between the scrobes and a little more transverse ; mesonotum more coarsely punctured ; scutellum unmargined laterally ; propodeon more densely punctured and striate basally ; the first segment of the abdomen a little less elongate and less raised in the middle, with the median groove weak.

This species bears a marked resemblance in colour only to *E. immaculata*, Krieg. (=*diversor*, Morl.) from Viti Levu, the largest island of the Fiji Group.

MOISTURE AS THE FACTOR AFFECTING WING DEVELOPMENT IN THE CITRUS APHIS, *TOXOPTERA AURANTII*, BOY.

R

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Introduction.

It is a well established fact that certain groups of Aphids, under various conditions, develop migratory alate forms which are capable of flying and seeking another host. Some writers contend that this phenomenon is associated with the life-cycle of the insect and that hereditary factors of alternation of generations have a bearing upon it. Mason (1923), for instance, says that the young Aphid, when born, has its adult condition as regards presence or absence of wings already determined and that the effect of environment has no bearing on their development—at least in the first generation. Other writers, however, claim that the cause of wing production lies in the environmental factors such as light (Shull, 1928), crowding (Reinhardt, 1927), etc.

On the other hand, it is pointed out that this wing development is the result of some physiological changes in the host-plant. Shinji (1919) writes that certain chemicals, when introduced into the food-plant of Aphids, possess the property of causing the development of wings. He even classifies the chemicals into wing-producing and non-wing-producing chemicals. He also believes that the chemical changes which take place in the plant during the late autumn cause wing development in Aphids. Haviland (1921) does not agree with these contentions and states that it is the inadequate diet which is the real cause for wing development.

Each of the above writers claims to have produced, through experiments, alate forms by such means as he specified. Nevertheless, there still exists an uncertainty as to what is after all the cause of this phenomenon. Very often, in order to avoid this issue, all these factors are referred to under the collective term of " unfavourable conditions." The present writer experimented with some of the wing-producing factors mentioned in the literature, such as reduction or complete interruption of food supply, crowding, temperature, humidity, etc. As a result of his studies, he was led to the conclusion that there is one basic factor which predominates over all other conditions that bring about the development of wings. Before discussing the experiments of others, the writer's own work will be described.

Methods of Breeding.

A short description of the breeding methods are given here in order to facilitate the understanding of some of the experiments. *T. aurantii* was bred on very young citrus twigs, the lower ends of which were placed in the water and the uppermost herbaceous end, upon which the Aphid was placed, was covered with a test-tube. By this method it was possible to observe each individual Aphid throughout its life and study its behaviour. It was also easy to place the insect in the desired condition of temperature. The Aphids were transferred to fresh twigs every two days or at periods varying in accord with the particular experiment. For the study of the effects of relative humidity on the insect, it was bred in conditions described later on under that caption.

Effects of Temperature.

The Aphid was bred continuously for over two years at a range of temperatures varying from 14°C. to 32°C. Various effects of temperature on the insects and their development were recorded, but no effect on wing production was observed. At times, low temperature, through the retardation of the development of the insect, offered more favourable conditions for other factors to exert their influence on wing production ; or on the other hand, high temperature, through accelerating the development of the insect, prevented other factors from influencing wing production. However, these effects of the temperature were incidental, and no direct influence on the development of wings in Aphids can be ascribed to temperature alone.

Effects of Crowding.

In the course of breeding the insect, it was observed that when larvae were allowed to remain in large numbers on the same twig, many of them developed into alates. In one case, for instance, about 112 larvae were not transferred to fresh food but were permitted to reach maturity on the old, stale twig upon which they were born, with the result that 15 matured into apterates, while 97 developed wings. However, as will be seen later, it was not the crowding that caused this high percentage of winged individuals, but another factor, which may be seen from the two following experiments :—

Fresh twigs were chosen, care being taken to have all of approximate size and state of maturity. Twenty-five first instar larvae were distributed on five twigs, five individuals on each, while 25 other larvae of the same lot were crowded within a length of 3 cm. on one twig. The result was that in both cases they developed into apterate individuals without any alates.

In another experiment 30 individuals were placed on a twig within a space of 5 cm. and 30 other individuals of the same age and lot were placed on another twig, crowding them into a 2 cm. space. The results were that the number of alates in the second lot was far less than in the lot where more space was allotted them. When the same experiment was repeated with 50 individuals on each twig, similar results were obtained (Table I).

TABLE I.

Number of individuals	Space allotted to them	Number of dead individuals	Surviving apterates	Surviving alates
30	5	6	17	7
50	5	25	14	11
30	2	15	13	2
50	2	8	38	4

From the above it may be surmised that crowding in itself does not cause wing development.

Effects of Stale Food.

A more decisive factor in causing the development of wings appeared to be the state of staleness of the food. It was observed in the course of breeding the insects that when larvae were permitted to feed on the food upon which their mother was feeding, the number of alates was quite high. On the other hand, when fresh food was given to the newly-born larvae and changed every two days, alates were never developed.

Special breeding experiments regarding this phase were carried out and the results are given in Table II A. It is clearly shown therein that on stale food the percentage of alates was quite high and that the number of such forms decreased when fresh food was supplied to the young larvae.

TABLE II.

Ratio of Apterates to Alates in Aphids feeding on stale and fresh Food respectively during December (A), *January and February* (B).

A.

Date	Feeding throughout their development period on Stale Food.			Transferred during the first instar on new Fresh Food.		
	Number of breedings	Surviving apterates	Surviving alates	Number of breedings	Surviving apterates	Surviving alates
1–8.xii ...	5	69	25	2	76	9
9–11.xii ...	4	30	20	1	18	1
13–16.xii ...	3	26	30	1	13	0
18–21.xii ...	3	25	24	6	47	1
23–26.xii ...	4	28	37	6	19	3
TOTAL ...	19	178	136	16	173	14

B.

JAN. & FEB. ...	7	106	5	2	74	1

It was further noticed that when the food was changed once at the beginning of the larval development, it did not matter much afterwards whether the same food was kept throughout the rest of the period or not. In the sixteen breedings mentioned in Table II A, in which fresh food was given to the young larvae, it was so arranged that in some breedings the food was not changed again, while in the others the food was changed every two days. The results given below (Table III) indicate that the difference in the proportion of apterates to alates is quite negligible.

TABLE III.

Conditions of feeding	Apterates	Alates
Food changed regularly every two days	64	4
Food changed only once	109	10
Total	173	14

This is due first to the fact that the process of wing development begins at the earlier stages of larval development and that at that critical time all larvae fed on fresh food ; secondly, the entire development period of the insect at the prevailing temperature was quite short and the food when changed even once was kept sufficiently fresh throughout the period.

There may be two reasons why stale food caused wing development : (*a*) the food obtained by the Aphids from such twigs is insufficient ; (*b*) there may have been plenty of food ingredients but the water content was too low. When a very vigorously growing, succulent twig was chosen as food for the Aphids, it did not produce many alate individuals, despite the fact that it was stale. Thus, no alate forms were developed among the Aphids feeding on the twigs cut during January and February at a time when the trees began to develop new growth, although the twigs were kept under the same conditions as those during the month of December. Table II B shows that only about 5 per cent. of alates were produced during these months, owing to the fact that the twigs remained fresh and succulent even a week after they had been cut. That this was not due to seasonal factors may be gathered from the fact that alate forms were obtained during this period by other methods as outlined below.

Effects of Wilted Food.

A high percentage of alates was obtained in the following breedings : The twig, although fresh, was allowed to dry one day and was placed in the water the following day and thus alternated until the Aphids reached maturity. In six breedings carried out during the latter part of the month of March and early April, 48 alates developed as against 63 apterates, while in the control—*i.e.*, where the twig was never removed from the water, 10 alates developed as against 111 apterates.

These facts lead to the belief that the loss of water, rather than the amount of food ingredients ingested by the Aphid, exerts a great influence on wing development. When the twig was removed from the water, it may have lost some moisture, but the remaining juice became more concentrated and the small amount ingested by the aphis may have contained more food ingredients than the diluted juice of the fresh plant. Therefore, it may be concluded that not the amount of food, but the amount of water in the food effects wing development. Furthermore, it is not the water content of the food itself but the water balance in the body of the insect which is the decisive factor. Regardless of how much water an Aphid may ingest with the food, if the evaporation of water from its body is too great, the effects are the same as if the intake of the water was too slight. This belief is based upon the following experiments and observations.

Effects of Relative Humidity.

Two sets of twigs with the same degree of succulence were chosen and small numbers of Aphids placed on them. While one end of the twig was placed in the water, the other end upon which the Aphids were feeding was placed in small fly trap-jars in which the relative humidity could be controlled by means of substances placed in the trap-jar. One set of Aphids was reared at a relative humidity of over 95 per cent. and the other set at a relative humidity of below 10 per cent. The results are given in Table IV, from which it may be seen that the ratio of apterates to alates is 10 : 1 when they are reared in a moist chamber, and 2 : 1 when reared in a dry chamber.

In another experiment insects of the first instar were removed from their food-plant and placed in small test-tubes, 20 larvae in each tube. They were allowed to remain without food for 24 hours. However, while one set of these tubes was kept in a room whose average humidity at that time was about 70 per cent., the other set was placed in a moist chamber with a humidity of about 98 per cent. At the end of the 24 hour period the insects were replaced on twigs and allowed to feed freely. Although both sets were permitted to remain without food for an equal length of time, the rate of alates to apterates did not coincide in the two sets, as is shown in Table V.

From this it can be seen that the smaller percentage of alates in the Aphids of the moist chamber was due to the fact that the water loss from their bodies during their abstinence from food was greatly reduced, a fact which substantiates the idea that the water balance in the body of the insect has a decided influence on wing production.

TABLE IV.

Effects of Relative Humidity on Wing Formation in Toxoptera aurantii.

Date of experiments	Twig placed in relative humidity below 10 per cent.			Twig placed in relative humidity above 96 per cent.		
	Number of individuals	Number of surviving apterates	Number of surviving alates	Number of individuals	Number of surviving apterates	Number of surviving alates
14.iii ...	20	0	4	20	17	0
17.iii ...	15	4	1	15	11	0
20.iii ...	25	17	2	25	24	0
22.iii ...	25	14	3	25	23	1
25.iii ...	25	9	13	25	17	5
25.iii ...	22	3	7	—	—	—
27.iii ...	21	14	9	25	17	6
29.iii ...	25	22	3	25	23	2
31.iii ...	16	10	2	12	12	0
	—	93	44	—	144	14

TABLE V.

Effects of Atmospheric Relative Humidity and Lack of Food upon Wing Development of T. aurantii.

Conditions of breeding	Apterates	Alates	Percentage of alates
Young larvae placed without food in humid containers	81	20	24·7
Young larvae without food remained in humidity of about 70 per cent.	56	44	78·5

Field Observations.

In addition to these laboratory experiments, some observations in the field should be recorded. Migratory females settle on very soft twigs only. It was observed that as soon as the twig grows, matures and becomes less succulent, the larvae born thereon tend to become alate and leave it as soon as they can fly. The percentage of nymphs that become alate is greater on an old, mature leaf than it is on a young, growing tip of a twig. The reason for this is probably due to the difference of the water content in such parts of the plant.

In Palestine during the spring and autumn very dry desert winds often occur. During such periods the relative humidity drops to 30–40 per cent. and not infrequently even to 10–20 per cent. It was observed that the larvae surviving such a wind—which is often detrimental to the life of the insect altogether—develop wing-pads. Naturally, it may be claimed that under such conditions the evaporation of water by the tree itself is great, and the food contains less water. However, in view of the experiments mentioned above, the writer is inclined to believe that the evaporation of water from the insect itself is also a dominant factor in this phase. A rich supply of succulent food with a large amount of evaporation from the insect will bring about the same effects as when the food supply is less succulent but the evaporation of water from the insect is reduced.

Intermediate Forms.

Naturally, since wing formation in Aphids depends upon the conditions of moisture in their food and environment, it may be asked what will be the outcome if conditions favouring wing formation alternate with conditions unfavourable to it. It was previously mentioned that the turning point in the development of alates or apterates takes place in the early stages of the insect. If, at this particular stage, conditions do not favour wing development, the insect tends to become apterate even though conditions may change afterwards and favour wing development. However, when conditions favouring wing development set in first, and the insect begins to develop wing-pads, and then food conditions improve—for instance, when very rich, succulent food is given to the Aphids—the development of the wing is checked and the individual matures into the so-called intermediate forms, *i.e.*, mature females with undeveloped wing-pads. Of the 29 Aphids that were bred by the writer under such conditions, all developed into intermediate forms.

Discussion.

With these ideas in mind, the literature on the subject may now be discussed.

It is quite possible that if Aphids become alate towards the end of the summer, it is due to the reduced amount of water in the leaves before leaf-fall.

With Aphids alternating their host-plants, it is an established fact that the migration or the appearance of an alate generation occurs after the plant has finished its growing and is about to wither or drop its leaves ; in other words, migration occurs at a time when the water content of the plant is reduced.

The rôle of some of the so-called wing-producing substances mentioned by Shinji (1919) was disproved by Haviland (1921), who could not produce winged Aphids by applying magnesium sulphate to the plant. However, in the light of the above-mentioned idea, namely, that the water balance in the body is the causal agent for wing development, it is worth while pointing out the probable reasons which brought about the results upon which Shinji based his conclusions. The heavy metals and magnesium sulphates contained in the solution to be absorbed by the rose twigs were probably detrimental to the plant tissue and the ends of the rose twigs were destroyed, so that the absorption of water was impossible. Thus the cutting off of the water supply probably caused the development of winged adults. On the other hand, the other substances did not interfere with the absorption of water by the plant so that they were able to produce apterous Aphids. Again, the sugar solutions which Shinji classified as wing-producing substances were perhaps detrimental to the tissues and destroyed them, or else the solution may have been too concentrated, thus preventing the absorption of water through osmotic pressure.

If Mason (1923) failed to obtain winged forms in his breedings in Florida, it may have been as a result of the high percentage of relative humidity prevailing in Florida causing little water loss from the Aphids which he reared. As mentioned above, such conditions do not favour wing development. The range of relative humidities at which Reinhardt (1927) carried out his breedings was insufficient to draw any conclusions therefrom. The experiments of the present writer showed that atmospheric relative humidity does influence this phase of the biology of *T. aurantii*. Crowding does bring about wing-formation in Aphids ; the experiments of the writer substantiates the assertions of Reinhardt. However, this is not due to the crowding in itself but to the inadequate supply of water and food. When 10 Aphids feed on one twig each one obtains a larger share of moisture and food than when 100 Aphids feed upon the same twig.

In the experiments of Markovitch (1921) and Shull (1928), regarding the effects of light upon wing development, there were too many contradictory factors involved. Too much exposure to light influences evaporation of the water by the plant, and changes in the water content of the food takes place. Again, when Aphids were removed from the plant and kept in darkness the factor of evaporation of water from their bodies without replacing it by feeding entered into the experiment, etc. Hence the contradictory results obtained by Shull. Weber (1930), in summarising these factors, states that light and temperature are interdependent, as well as relative humidity, precipitation, growth of plants and nourishment ; all these factors have equally a definite influence on wing production. In view of the facts brought forth in this paper, a correction should be made to Weber's summing up of facts, namely, all these factors mentioned by him and other students exert directly or indirectly an influence on the water content of the insect body, which in turn is the real cause of wing development in the Aphids.

Summary.

1. Temperature does not affect wing development in Aphids.

2. A great percentage of Aphids developed wings when they were crowded, or when they were forced to feed on stale or wilted food. This was due to the small amount of food and particularly of water which each individual Aphid obtained.

3. A reduced percentage of water in the food of Aphids, as well as a low atmospheric humidity, are primary factors causing wing development.

4. All the factors such as light, temperature, crowding, humidity, precipitation, growth of plant, etc., exert, directly or indirectly, an influence on the water balance in the body of the Aphid, which in turn causes wing development.

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NOTES ON THE LIFE-HISTORY OF *CHEILONEURUS NOXIUS*, COMPERE (HYM.).

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A number of species of this genus of Encyrtid parasites are known to be, and others are suspected to be, secondary parasites; but apparently the complete life-history has not been observed in any one case. As the genus has an almost world-wide distribution and is doubtless of considerable economic importance, the following observations made in Southern California* in part of 1935 and 1936 are recorded.

The species studied, *Cheiloneurus noxius*, was described by Compere[1] originally from three females collected in Pasadena, California, in 1923, the same author later describing the male from collections made in Riverside, California[2]. In this paper the following biological note is added " *Cheiloneurus noxius* Comp. is presumably hyperparasitic although we have no positive evidence to this effect." Details of the life-history of another species, *Cheiloneurus inimicus*, Comp., were recorded by Compere[1], who observed the phenomenon of the increase in size of the egg before hatching, similar to that now recorded for *Ch. noxius*. The first and second larval stages of *Ch. inimicus* were also observed and figured.

A few individuals of *Ch. noxius* were first obtained from cages containing *Saissetia oleae* (Bern.) parasitized by several species of primary parasites including *Metaphycus lounsburyi* (How.), which was the host on which the *Cheiloneurus* was studied. The temperature of the room in which the observations were made fluctuated between 15°C. and 25°C. The outlines of all drawings were made with an Abbé camera lucida, other details are somewhat diagrammatic. The scale is indicated in each case by a line representing 0·1 mm.

The female *Cheiloneurus* explores the scale with tapping antennae, then mounts on it and may immediately begin to insert the ovipositor. The scale is pierced apparently by a partial rotation of the ovipositor with considerable pressure exerted on it from above by the parasite. The boring through the scale was observed to take from one to fifteen minutes, according to the hardness. After the scale is pierced the ovipositor is completely inserted, and if the contents of the scale are liquid it is usually withdrawn immediately. Otherwise it is used to probe the interior of the scale in search for the larva or pupa of a primary parasite. The probing and oviposition usually take one or two minutes. The insect wastes considerable time in boring through scales which are not parasitized and attempting scales which prove too tough.

The ovarian egg has a long stalk dilated at the end, as shown in fig. 1 A. It is deposited free in the body of the primary parasite and for a number of hours it retains approximately the shape of the ovarian egg, though the stalk and swelling are proportionately smaller, as shown in fig 1 B. The incubation period in the conditions prevailing was from 4 to 5 days, and during this period the egg undergoes considerable enlargement, as shown in fig. 1 C, D, E, during which the stalk appears to shrivel, showing hardly at all at the time of hatching. As the egg is deposited loose in the host, the stalk does not seem to have any respiratory function; it probably assists in allowing extrusion through the slender ovipositor. Just before hatching the larva can be clearly perceived inside the egg, the tail being directed

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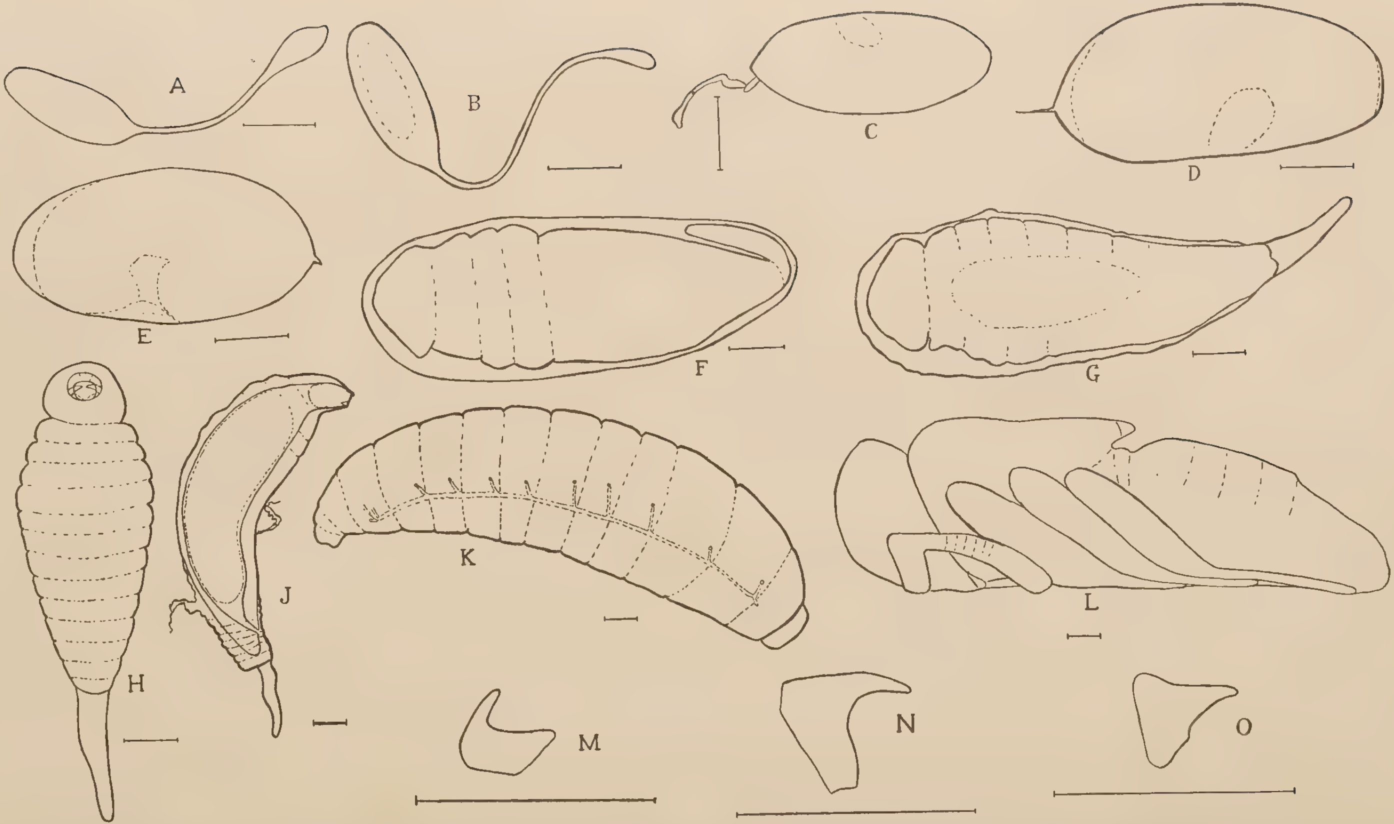

Fig. 1. A, ovarian egg ; B, egg three hours after laying ; C, egg 44 hours after laying ; D, egg three days after laying ; E, egg four days after laying ; F, egg just before hatching, five days ; G, same egg immediately after hatching ; H, first instar larva ; J, second instar larva ; K, third instar larva ; L, pupa ; M, mandible of first instar ; N, mandible of second instar ; O, mandible of third instar.

forward and folded against the body (fig. 1 F). In several instances after eggs had been removed from the host on to a slide the tail was seen to spring instantaneously from this flexed position, breaking the chorion in doing so. It seems likely that this is the usual means by which hatching takes place. Fig. 1 G was drawn from the same individual a few minutes after fig. 1 F, when the chorion had been ruptured in this manner.

The first-stage larva eventually frees itself completely from the egg; it has a well marked head, thirteen body segments and the tail (fig. 1 H). It remains in this stage from 2 to 3 days. The second-stage larva is shown in fig. 1 J; in this stage the skin of the first-stage larva remains attached to the posterior segments. The larva is in the second stage from 2 to 4 days. The third-stage larva, shown in fig. 1 K, has lost the marked head and the remains of the first-stage tail are gone, though it is usually possible to see the remains of the first and second-stage skins for some time at least. The third larval stage lasts from 3 to 5 days. The pupal stage lasts from 4 to 6 days. Fig. 1 L gives a lateral view (camera lucida outline, remainder diagrammatic) of the pupa of the female which shows the distinct projection that corresponds to the tuft of setae on the scutellum of the adult female. The mandibles of the three larval stages are shown in fig. 1 M, N, O.

The life-history from the laying of the egg to the emergence of the adult at a fairly constant temperature varying between 32°C. and 27°C. may occupy as little as 14 days. In cases observed, virgin females produced only male offspring. The primary parasite *Metaphycus lounsburyi*, on which *Cheiloneurus* was reared, may develop to maturity in large numbers in an individual scale of *Saissetia oleae*, as many as eighteen having been observed on more than one occasion to develop in one scale, while ten or twelve is not uncommon. *Cheiloneurus* will on occasion deposit more than one egg in an individual host larva, and two *Cheiloneurus* larvae have been observed in one host, though in no case has more than one been known to develop to maturity. But each of the primary parasite larvae or pupae may be attacked, and in one case eleven *Cheiloneurus*, four females and seven males, emerged from an individual scale, no primary parasites emerging in this case. From a number of records of the emergences from single scales the following are chosen; 5 *Metaphycus* and 4 *Cheiloneurus*, 10 *Metaphycus* and 4 *Cheiloneurus*, 1 *Metaphycus* and 5 *Cheiloneurus*, 2 *Metaphycus* and 7 *Cheiloneurus*. One hundred scales which had been exposed to attack by *Metaphycus* were later exposed to several *Cheiloneurus* for twenty-four hours, and the numbers of parasites that emerged from 86 scales attacked were 393 *Metaphycus* and 151 *Cheiloneurus*, and of the latter 76 were females and 75 males.

In the field *Cheiloneurus noxius* is not usually abundant, and it is not considered to interfere seriously with the beneficial activities of *Metaphycus lounsburyi*.

The writer desires to thank Professor Harry S. Smith for facilities kindly accorded.

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NOTES ON THE ECOLOGY AND CONTROL OF PINE BEETLES IN GREAT BRITAIN.

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(Plates VI–VIII.)

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I. Introduction.

This paper is intended to be a preliminary survey of the ground to be covered by an investigation which is being carried out in connection with the study of the possible methods of control of injurious insects in pine areas in Britain, with a view to the reduction or prevention of the damage which is caused by these insects, with special reference to the pine beetle, *Myelophilus piniperda.*

In preparing the scheme of work, it was found impossible to deal adequately with the control of *Myelophilus* without taking into consideration the possible effects such measures might have on the other pine beetles, particularly those of the genus *Hylastes*, and also the pine weevils, *Hylobius* and *Pissodes*, since any control measure designed to combat *Myelophilus* that favoured the increase of any of the other pests would be fatal to the success of the scheme. It became evident that the only satisfactory way to deal with the problem was to include the whole biological group within the scope of the operations. Fortunately, only a few of the British pine beetles are of great economic importance; of these *Myelophilus* *piniperda*, L., *M. minor*, Hart., and *Hylastes ater*, Payk., are the most destructive. Of the pine weevils, *Hylobius abietis*, L., is by far the most important. Probably everyone interested in forestry is familiar with some of the main facts in the life-histories of these four insects, as forestry literature is full of references to them and various detailed accounts of the biology of each species have been published from time to time. There are considerable differences between some of these accounts, indeed, in some cases they appear to be contradictory, and a certain amount of confusion exists. This is largely due to the fact that the breeding habits of the various species are not constant, but are influenced by several factors, or combinations of factors, the precise nature and extent of which have not yet been definitely ascertained. Consequently, the behaviour of the insects does not conform to any orthodox or stereotyped life-history.

Because of the inter-relationship which exists between the feeding and breeding habits of these species, and the frequency of the occurrence of their combined attack on the host-plant, they form a biological association which is a menace to the profitable cultivation of Scots pine in Britain. In all cases the feeding habits of the insects concerned are the primary cause of the destruction ; this is due to the fact that in each case the living tissues of the host-plant are attacked. The breeding habits are closely associated with the feeding habits and combine to complete the destruction of the tree.

Although all four species will breed in the bark of felled trees, they readily attack living trees ; the degree of activity of the cambium layer of the tree and the intensity of the attack are, in each case, the limiting factors which determine whether the attack is successful. If the vitality of the tree is reduced, from whatever cause, to a sufficiently low level, the insects are able to breed successfully in the bark, and the complete destruction of the tree rapidly follows. The material remains suitable for breeding purposes so long as it is fairly fresh, but once it becomes dry and the bark becomes loose, or is invaded by fungus, it is no longer suitable for breeding.

The reduction of the vitality of the tree may be brought about by a variety of causes. The pine beetles are, themselves, sometimes responsible, *Myelophilus* feeding in the shoots in summer, or in the bark at the base of the tree in winter, or a combination of the two may, if the infestation is very strong, result in the bark of the stem becoming suitable for breeding purposes. *Hylastes* and *Hylobius* breed in the bark at the base of the stem or in the roots. In the case of mature trees the cycle sometimes begins with the attack of these species on the roots, and is followed by *Myelophilus* on the stem. The attack on the bark of the stem by *Myelophilus* sometimes follows the attack on the roots of the tree by fungus, but it is not yet known to what extent the attack of the fungus is due to the previous attack of *Hylastes*.

The chief damage done by *Hylastes* is in feeding in the bark of young trees at ground-level, or on the roots, but the attack on the root is not confined to young trees.

Hylobius is most destructive in young plantations, by feeding on the bark of young trees just above ground-level, and it also feeds on the bark of the twigs and branches of older ones. In practice, the control measures are designed to deal with both the pine beetles and the pine weevils, but for convenience in writing up the results, the pine weevils will be dealt with in a separate paper.

II. THE ECONOMIC STATUS OF THE PINE BEETLES IN BRITAIN.

The pine beetle problem in Britain differs considerably from that of many other countries. In this country the majority of our pine areas are comparatively small and scattered, and are, in theory, worked on a more or less regular system. Portions of each block of forest are cleared and other portions replanted each year, so that the areas consist of a number of crops of various age classes growing side by side, or at some distance apart from each other. Consequently, the pine beetle population varies considerably in various parts of the forest or pine areas in any particular district. A different set of conditions exists in each case and the level of the pine beetle population fluctuates considerably. Sporadic outbreaks occur whenever favourable conditions arise, and the dispersal of the insects results in a general rise of the bark-beetle population in surrounding areas. It will be seen, therefore, that the problem of bark-beetle control in Britain necessitates a careful detailed study of all the factors which tend to influence the increase or decrease of the bark-beetle population under any particular set of forest conditions. Its object must be to prevent any sudden increase and to maintain the pine beetle population at such a low level as to prevent damage being done. Control measures must, therefore, be of a very intensive character.

In some countries where large tracts of natural forest still exist and there is an abundance of material from which to select timber or poles for special requirements, the necessity for special detailed control measures to prevent structural defects in the trees has not yet arisen. Insect infestations in these countries are generally classified as either endemic or epidemic, and only when the infestations fall in the latter category is it considered necessary to apply control measures. The most severe forms of epidemic are generally associated with large-scale felling operations, windfalls or forest fires, and as these infestations are often on a very large scale, only the most serious cases can be dealt with, and control measures are therefore on a correspondingly large scale. Infestations of endemic status are not considered of sufficient importance to warrant the necessary expenditure under present economic conditions ; the losses incurred by endemic infestations are therefore accepted, and control measures are concentrated on the restriction and termination of epidemics and the prevention of the complete destruction of large tracts of forest. With the disappearance of the over-mature natural forests, a more intensive system of forestry will be necessary, and the pine beetle problem will then more closely resemble our own. Sweden is probably the best example of this transitional stage.

In the case of an annual crop, insect damage can be assessed ; whatever loss has been sustained is apparent at the time and the grower knows the exact position from year to year. Unfortunately this is not possible with forest crops. Injury which may appear slight, or may even pass unnoticed, may have a very serious effect on the value of the final crop. Moreover, the effect of the injuries are cumulative ; a succession of slight injuries may result in a considerable financial loss at the end of a long rotation ; while more severe attacks may prove disastrous and result in a worthless crop, the proceeds from which scarcely cover the cost of felling, removal and replanting. The low financial returns prejudice woodland owners against Scots pine, in favour of exotic species, many of which produce timber of inferior quality, but entail less risk. The various types of malformation have become such familiar objects that they are generally regarded as normal features of the tree's growth and are often accepted as more or less inevitable.

The injuries caused by *Myelophilus* are of a permanent character and the record of the insect's attack is indelibly stamped on the tree and form a somewhat striking analogy to fossil remains in geological strata. By means of careful examination of the external characters and a detailed analysis of the stems of a large number of trees, it is possible to read the history of *Myelophilus* attack and by the collection of a sufficiently large amount of data of this character, it will be possible to ascertain the extent of the various types of damage and assess the loss incurred. The assessment of this loss forms part of a separate investigation and does not therefore concern us here.

However, before it is possible to formulate measures for the control of the pine beetles, it is necessary to ascertain the exact nature of the various types of damage.

III. Analysis of Damage.

The types of damage caused by the attack of *Myelophilus* may be classified as follows :—(1) The formation of " kinks " in the stem of the trees ; (2) limitation of the length of the timber ; (3) general limitation of the height growth of the crop ; (4) the formation of " spire tops " ; (5) destruction of immature crops ; (6) winter feeding ; (7) loss of increment ; (8) trees killed which have been slightly injured by fire ; (9) hastening the death of suppressed trees ; (10) hastening the death of mature trees ; and (11) the destruction of seed trees.

Type 1. *The formation of " kinks " in the stem of the trees.*

When attacking the shoots of pines, *Myelophilus* definitely prefers the upper portion of the crown where the shoots with the largest pith are to be found. Consequently, the leading shoot is among those most frequently attacked. A vigorous leading shoot may contain a dozen or more beetle tunnels before it finally breaks off, although one tunnel is often sufficient to cause the damage. If the leading shoot is replaced by a side shoot of the same year's growth, the consequences of the injury may not be very serious, the new leader straightens out, and the slight irregularity in the stem is almost entirely effaced by the layers of wood formed in subsequent years. Plate VI, fig. 1 shows a first-year recovery.

In the specimen shown in Plate VI, fig. 2, the lost leader was replaced by two new leaders of the same year's growth, but both these leaders were destroyed in the succeeding year and were superseded by a leader arising from a previous year's growth. In this case the new leader is unable to straighten out completely and a " dog-leg " is formed. The layers of wood laid on subsequently might ultimately obliterate the defect, but if the tree is felled any time before that stage is reached, there will be a " kink " in the stem at the point where the new leader was formed. If the tree is required for use as a telegraph pole, it is rendered unsuitable for the purpose. Plate VI, fig. 3, shows this type of defect.

The frequency with which these kinks occur in poles, which are otherwise suitable for telegraph poles, has during recent years focussed the attention of the Forestry Commission on this aspect of the damage, and on the desirability of studying methods for the control of *Myelophilus*.

Type 2. *Limitation of the length of the timber.*

The loss of the leading shoot in a strong, vigorously-growing dominant tree may result in two or more new leaders being formed. Plate VI, fig. 4 shows the formation of a forked tree owing to the loss of the leading shoot and the whole of the first whorl of branches as a result of the attack of *Myelophilus piniperda*. The development of three leading shoots resulting from the loss of the original leader is shown in Plate VII, fig. 1. This may ultimately result in a triple-crowned tree. A section of one is shown in Plate VII, fig. 2.

This type of damage frequently occurs immediately after a heavy thinning and may be caused by the beetles that emerge from the poles which have been felled in the thinning and left during the breeding season. By the time the crop is due for the next thinning, these trees may have developed into what are termed " wolf " trees. If they are not very numerous and the crop is still young and fairly dense, these trees may be removed in the subsequent thinning ; inferior trees, which would otherwise have been removed, being left to take their place. If, however, this type of damage is very prevalent, it is impracticable to remove all the injured trees, especially when the crop is in a fairly well-advanced stage of growth, or, as frequently happens, if the situation is aggravated by the fact that the density of the crop has already been reduced to a minimum by the removal of "posthorn" trees, resulting from the attack of the Pine Shoot Moth (*Evetria buoliana*, Schiff.), a form of injury only too prevalent in the early stage of the crop's development, and one which often claims precedence of attention during the first thinning.

Forked and multiple-crowned trees are very common in crops in Britain. In fact, we have become so accustomed to this type of tree, that it is, by many people, regarded as the natural habit of Scots pine. When the mature crop is felled, unless exceptional lengths are required for special purposes, and provided he can get 20 feet to 30 feet of clean timber in the butt, the timber merchant generally welcomes a "stop" or "break" in the measurement of the stem, and in the valuation of standing timber everything above that point is regarded as valueless. The effect of this limitation in the length of the timber is often disastrous to the financial yield of the final crop.

Squirrels frequently cause the loss of the leading shoots of pines and bring about the same results, and where squirrels are numerous much of the damage actually done by *Myelophilus* is probably attributed to them.

Type 3. *General limitation of the height growth of the crop.*

Owing to the beetle's distinct preference for the upper portions of the crown for feeding purposes, the dominant trees suffer much more heavily than suppressed trees. When a severe infestation takes place, it not infrequently happens that every terminal shoot is destroyed on the whole of the higher whorls of branches, and a new leading shoot arises from a lower level, producing a combination of the two types of damage already dealt with, but on a large scale, resulting in a reduction in the height of the crop by several feet. This type of damage is much more common than is generally supposed. In the case of the specimen shown in Plate VI, fig. 1, the leading shoot was destroyed by *Myelophilus* in the year 1930 and was replaced by another shoot of the same year's growth. In 1934, the leading shoot was again destroyed and 13 separate *Myelophilus* tunnels were counted in the shoot. At the same time every terminal and lateral shoot on the whole of the branches produced during the last five years was destroyed. It will be seen, therefore, that replacement of the leader in 1935 would have to take place from the whorl of branches formed in 1929, resulting in loss of height growth. The effect of this sixth year recovery would be an exaggerated form of the malformation shown in Plate VI, fig. 2. Superseded leaders of several years' growth are often finally killed off by excessive shade and may frequently be seen in standing woods. Plate VII, fig. 3, shows an example.

The effect of a general setback in height growth as a result of a strong *Myelophilus* infestation may be seen in many woods in the form of a definite layer of defects or malformations of the stem, corresponding with the period when the infestation occurred. If strong infestations occur at intervals of several years, two or more strata of defects may be the result.

Type 4. *The formation of "spire tops."*

This type of damage seldom occurs over very extensive areas, but is generally confined to clumps or belts of trees, and strips along the edge of large stands, especially in the neighbourhood of open forest or heaths with self-sown pines, where fires occur from time to time. Plate VIII, fig. 1, shows part of a strip over a mile in length along the edge of Hawkhill Inclosure in the New Forest. This type of damage is caused by the repeated attack of pine beetles, which invade the stands from external breeding-grounds. The upper portions of the crowns are almost defoliated, height growth is completely arrested and the trees have "spire tops." Plate VII, fig. 4, shows a four-feet length of the top of one of these trees. The present Deputy Surveyor of the New Forest has considerably reduced the danger of this kind of damage by adopting the policy of clearing self-sown pines from the open forest in the neighbourhood of inclosures planted with pines. This form of damage is not, however, confined to the trees in the neighbourhood of open forest or burnt areas ; it is often found near country sawmills, timber dumps, or where extensive fellings have been carried out. It is the most conspicuous form of beetle damage where it occurs, and is popularly considered to be the only kind of beetle damage of importance, and its presence or absence is unfortunately often regarded as a criterion as to whether *Myelophilus* is numerous or otherwise in any particular locality. In the opinion of the present writer, this is a mistaken idea which is liable to lead to erroneous conclusions. The absence of " spire tops " affords no evidence as to the extent of other forms of damage, and does not necessarily indicate that *Myelophilus* is not abundant. In very extensive pine areas where no fires or large-scale fellings have occurred, there may be no sign of this form of beetle damage ; nevertheless, other forms may be prevalent. The fact that this form is generally confined to clumps, belts and strips of trees along the edge of woods, does not necessarily mean that it is of little importance. When strips of this type of damage occur along the edge of large blocks of Scots pine forest, they are seldom less than a chain in width and are often much wider, and it must be remembered that a strip one chain in width round the edge of a square ten-acre wood, represents 36 per cent. of the total area. While in the case of a square wood a quarter that size, a strip of one chain in width round the edge represents 64 per cent. of the area. If the shape of the wood is irregular, the relative area of the strip increases in proportion. In the aggregate there must be hundreds of acres of Scots pine woods in Britain completely ruined by this type of damage.

Although the trees are permanently prevented from ever forming a profitable crop, a large proportion of the foliage persists and a dense crown is often formed at a lower level, giving the appearance of renewed vitality. This is often referred to, sometimes with pride, as successful recovery from severe *Myelophilus* attack. There is no real recovery from this form of damage.

Type 5. *The destruction of immature crops.*

This type of damage seldom occurs in Britain, except on a small scale and it is possible only under exceptional circumstances. The danger is, however, always present, and with the extension of the area of the pine forests it becomes increasingly necessary to guard against the possibility of this kind of destruction.

Type 6. *Winter feeding.*

In the late autumn many *Myelophilus* adults tunnel into the bark at the base of standing trees and feed in the inner bark. Their presence can be detected by the little heaps of fresh meal-like dust or " frass " as it is sometimes called. Plate VIII, fig. 2 shows the base of one of a number of Scots pines which were attacked in the New Forest in November 1934. If the infestation is strong, this winter feeding may cause considerable damage. Trägårdh (1921) states that in an experimental plot 6 per cent. of the trees were killed and 6 per cent. were fatally injured in the course of two years. An examination of trees most heavily attacked did not furnish any evidence as to the reason why they were selected for breeding purposes. This winter feeding is probably a serious factor in reducing the vitality of the trees to a point where they are suitable for the breeding purposes not only of *Myelophilus*, but also of *Hylastes* and *Hylobius*.

Type 7. *Loss of increment.*

This loss is a direct result of the reduction of the assimilation area of the crown by the pruning effect of the summer feeding of *Myelophilus*. As the loss of increment is in proportion to the intensity of the infestation, it is probable that it is always of minor importance as compared with the malformation of the stems, which accompanies the cause. Nevertheless, loss of increment is of some importance. Mattsson

Marn (1921) has shown that in extreme cases the increase of the diameter of the tree may be lessened by 22 per cent. and that a 10 per cent. reduction entails a loss of about 1,600,000 cubic feet of timber in Sweden.

Type 8. *Trees killed which have been injured by fire.*

This type of damage is probably on the increase in this country. Each year many trees which have been slightly injured by fire, but might reasonably be expected to recover, are attacked by bark-beetles and killed. The loss incurred by the destruction of the injured trees is only one aspect of the damage ; these trees are liable to form the nucleus of an infestation, which may cause considerable damage in surrounding pine areas.

Type 9. *Hastening the death of suppressed trees.*

When a plantation is thinned, it is generally necessary to leave a fairly large percentage of the suppressed trees standing in order to maintain the required density of the crop and to preserve an unbroken canopy. *Myelophilus* frequently causes the death of many of these suppressed trees by attacking the bark for breeding purposes, and the crop becomes too open.

Type 10. *Hastening the death of mature trees.*

The death of mature Scots pine trees is often brought about by the reduction of the foliage by the feeding of *Myelophilus*, followed by the attack on the bark for breeding purposes. In many cases the attack of *Myelophilus* is preceded by the attack of *Hylastes* on the roots and the base of the stem at ground-level, and sometimes by *Hylobius*. In the case of ornamental and park trees, the actual financial loss is the least important aspect of the damage.

Type 11. *The destruction of seed trees.*

In the case of fellings, where seed trees are left standing to bring about natural regeneration of the crop, the beetles which emerge from the bark of the felled trees sometimes completely destroy the seed trees. Even if the trees are not killed their seed production may be seriously diminished. This type of damage is of considerable importance in some countries and may become of great importance in this country in the future, if steps are not taken to prevent it.

It will be seen from the analysis above that *Myelophilus* is the cause of many kinds of injury, each of which has the effect of reducing the revenue. Collectively, the various kinds of damage result in a great reduction in the value of the crop. A superficial comparison tends to give the impression that types 1 to 5 are progressive stages of increased intensity of the first, and that the importance of the damage is in increased ratio for each of the second, third, fourth, and fifth types. This is far from being the case ; each type of damage has its own particular significance, and although all five types may sometimes occur in the same group of trees, it does not necessarily follow that types 4 and 5 are always accompanied or preceded by 1, 2 and 3. In fact, types 4 and 5 generally have a totally different origin ; they usually result from an invasion of the stand from outside, while, on the other hand, types 1, 2 and 3 develop within the area. Type 1 is the most simple, subtle, and unobtrusive form of damage, and also the most widespread. It is the most elementary form and its elimination would automatically result in the eradication of all other forms. In fact, its elimination is impossible while other forms are allowed to occur. *Myelophilus* cannot be regarded as being under economic control while this type of damage exists in Scots pine stands. The presence or absence of kinks due to *Myelophilus* may, therefore, be taken as a criterion of the economic control of this insect.

As Dr. W. R. Thompson (1930) has pointed out : " Whether an insect pest is in control from the standpoint of the economist depends upon whether the injury resulting from its presence causes a financially measurable loss."

IV. THE OCCURRENCE OF OUTBREAKS.

Myelophilus piniperda is present in all Scots pine areas in Great Britain. The beetle, in common with other species of pine beetles, may, in fact, be present in considerable numbers without attracting attention. From time to time circumstances arise which favour rapid increase and pine beetle outbreaks occur. These outbreaks may, for convenience, be divided into four distinct types, occurring in either natural woods or plantations :—(1) The periodic outbreak before thinning ; (2) in natural pine areas or plantations where thinnings are being carried out ; (3) following clear felling and windfalls ; and (4) in areas injured by fire.

The periodic type of outbreak occurs from time to time in most pine areas, probably in all natural forests. Even in very young plantations which have not yet reached the thicket stage, it is generally possible to find a few trees which have become sickly and died from one cause or another, often through drought, water-logging of the soil, and attack on the roots by insects or fungi, bad planting, injury by voles, or from some other cause. These trees may be attacked by *Myelophilus* and other bark-beetles, and serve as breeding places. When the crop reaches the thicket stage many trees fall behind in the struggle for existence and are killed through excessive shade. If the necessary thinning is not carried out the available breeding material rapidly increases, owing to the increased number of trees which are suppressed and become suitable for breeding purposes. The period of maximum density is followed by an opening up of the crop for a time, and as the surviving trees increase in size, another period of maximum density is reached. The periodic outbreak of bark-beetles probably coincides with the time immediately following the periods of maximum density, that is to say, when the greatest quantity of suitable breeding material is available. This type of infestation results in an enormous amount of damage of types 1, 2 and 3. On some estates in Scotland no thinnings are carried out until the pines are 50 to 60 years of age, and large blocks of forest exist which clearly show the effects of the periodic type of outbreak.

The second type of outbreak occurs when heavy thinnings are carried out in pine areas which have been neglected too long, or where windfalls or extensive snow-breaks have occurred. If the material is not barked or removed the sudden increase of suitable breeding material favours the extensive increase in the bark-beetle population. The damage is aggravated by the fact that, owing to the neglect of thinnings, the canopy has become too dense and the crowns of the trees are dwarfed and are unable to withstand the extra cropping which takes place when the new generation of bark-beetle adults commence to feed. This type is in reality an exaggerated form of the first, but is often more disastrous because of the suddenness with which the artificial increase of breeding material precipitates the outbreak and replaces the slow natural thinning which normally takes place. The sudden cutting down of the majority of the suppressed trees causes a concentration of attack by the new generation of adult beetles on the crowns of the dominant trees for feeding purposes, and is followed in the autumn by winter feeding on a large scale at the base of the trees, and in the succeeding season by an attack for breeding purposes on the remaining more or less suppressed trees which have been left standing. Consequently, the result is worse than would have been the case if no thinning operation had been carried out, as not only a very severe form of the first, second, and third types of damage occur, but frequently also types 6, 7, and 9.

An excellent example of this type of infestation occurred in Sweden some years ago, when extensive thinnings of the forests were undertaken. Trägårdh (1918) stated that the common reports that pine beetles are spreading must not be taken literally ; they show, however, that owing to the thinning of the pine forests, which is practised to a greater degree every year, the facilities for the propagation of these pests have greatly increased.

The third type of outbreak occurs in areas where heavy felling operations are in progress. This type is frequent and destructive. Owing to the sudden increase of suitable breeding material concentrated on the area, the resident bark-beetles supplemented by others attracted from surrounding neighbourhoods produce a tremendous increase in the bark-beetle population. The beetles that emerge and form a new generation invade the nearest pine stand and produce the fourth type of damage and eventually contribute to all the other types of damage, since they later disperse throughout the whole area, and the general level of the bark-beetle population is greatly increased.

The fourth type of outbreak is becoming more frequent in Britain with the extension of pine growing, and in the future outbreaks as the result of forest fires may become a serious menace to pine areas in this country, unless steps are taken to deal adequately with the subject. The burnt trees are immediately available for breeding purposes and attract the bark-beetles from surrounding areas ; the next generation of beetles attack the crowns of the slightly injured or uninjured trees adjacent to the burnt area ; these trees in turn are severely weakened by the heavy pruning which takes place.

It will be seen from the above that the available supply of breeding material (*i.e.*, feeding material for the larvae) is the principal factor favouring the increase of *Myelophilus* and not the supply of food material for adult insects, as the whole of the pine forest is always available for the latter. It will further be seen that the feeding habits of the adult insects largely contribute towards the maintenance of the supply of suitable breeding material by weakening the trees by cropping the crowns in summer and attacking the cambium layer at the base of the stem in winter. The latter form of damage is much more common than is generally supposed. It is quite clear that owing to the inter-relationship of these highly specialised feeding and breeding habits, *Myelophilus* would, in the absence of controlling factors, rapidly increase to such an extent that the whole of the pine forests would be completely ruined.

V. Factors Influencing the Pine Beetle Population.

1. Climatic and Physical Conditions.

Among the factors influencing the increase of pine beetles, climatic and physical conditions are of fundamental importance. As the work of the investigation progressed, it became more and more apparent that the study of the effects of these factors on the development of the host-plant under forest conditions formed the key to the solution of the problem of bark-beetle control in pine areas, and it became evident that control measures could not be studied in their correct perspective until the direct and indirect effects of climatic and physical conditions had been studied in detail.

The available evidence suggests that the use of the term " vigorous growth," in connection with the vitality of trees is misleading when used to denote whether a tree is healthy or unhealthy. Increase in northern latitude, elevation, exposure, and poor soil conditions, may result in retarded growth ; and, in extreme cases, growth may be so diminished as to result in a stunted, scrubby condition rendering the trees entirely useless for timber production. Nevertheless, even under these extreme conditions the trees show no sign of being more attractive to insects, or more suitable for breeding purposes than trees grown under more favourable conditions. Nor can these trees be regarded as being lacking in vitality ; they are, in fact, extremely hardy.

In studying the results of insect attack in the formation of " kinks " and other malformations in the stem of Scots pine, it appears that the more rapid the growth of the tree, the more violent is its reaction to any irritant or injury, and the more exaggerated and distorted becomes the malformation resulting from certain types of injury.

Observations indicate that the more rapidly the pathological condition of a tree is brought about, the more attractive it is for *Myelophilus*, *Hylastes*, and pine weevils for breeding purposes. Consequently, trees which have hitherto been growing fairly rapidly, but have been killed by rapidly increased shade, are more attractive for breeding purposes than trees which have been growing slowly and have been killed by gradually increased shade. The reason for this apparently lies in the difference in the quantity and quality of the cell contents of the bast forming the necessary food supply for the larvae. This has a direct bearing on the development of insect populations in pine areas. The more exacting the conditions under which the crop grows the slower is the rate of growth of individual trees, and the greater the number of trees than can occupy an equal area of ground at any given age. The more rapid the rate of growth the greater the competition and the fewer the number of trees that survive at any given age. The difference in the number of healthy stems in the two types of crops represents the difference in the amount of breeding material which has become available for pine beetles and weevils. For example, at 50 years of age the average Scots pine crop grown in the south-east of England has a density of only 375 stems per acre, as compared with a density of 550 stems per acre in the case of the average Scots pine crop grown in Scotland. These figures show that in the more rapidly grown crop an additional 175 trees per acre have become liable to attack by pine beetles and weevils for breeding purposes. Moreover, since the more rapidly grown crop produces bigger trees at any given age, the total area of bark on the trees killed by excessive shade will be much greater in the case of the rapidly grown crop than the case of the slowly grown crop. It will readily be seen, therefore, that vigorous growth results not only in a crop consisting of fewer but larger trees, but also in the provision of larger quantities of suitable breeding material for bark-beetles and weevils.

Conditions favourable for rapid growth of the pine trees during the early stages of the crop's development result not only in the production of timber of inferior quality, but also in the reduction in volume per acre during the later stages. On the other hand, if the rate of growth in the early stages is retarded beyond a certain point, this may also result in a reduction in volume increment during the later stages.

Apart from abnormal increase brought about by exceptional breeding facilities as a result of fire, windfall, and felling operations, the conditions favouring the increase of bark-beetles and wood-boring insects in pine forests are considered to be mainly due to exceptionally favourable conditions for vigorous growth during the early stages of the crop's development, resulting in large numbers of trees being suppressed and killed in the pole stage by rapidly increased shade as a result of uneven growth and the abnormal development of predominant trees; this is inevitable when Scots pine plantations are formed on soils too rich and situations too favourable. Such soils and situations could with advantage be utilised for the growth of more exacting trees.

On the other hand, exceptionally favourable conditions for bark-beetle development occur when conditions are unfavourable for the healthy development of the crop owing to bad drainage conditions and water-logging of the soil. Such conditions are only too prevalent and it is impossible to over-estimate the importance of the necessity for attention to this subject.

2. The Factor of Overcrowding of the Beetle Population.

The effect of overcrowding as a factor in the limitation of the rate of reproduction, and as the cause, directly or indirectly, of heavy mortality among the bark-beetle broods, is a subject of considerable importance. Trägårdh (1934) gives some interesting figures with reference to this subject. He states that in 1932, the first year after the big windfall in Sweden, only 7 per cent. of the available bark area was utilised by bark-beetles, and that exceptionally large gallery systems were found instead of the normal. As a result of the abundant breeding space available and other favourable factors, as for instance the relatively low number of predators and parasites, the production per gallery, as was to be expected, was very high. In the second year (1933), owing to the greatly increased population, the available bark area was fully utilised, and the results are shown in the following table :—

TABLE I.

	Area (cm.) per gallery			Production per gallery			Production per sq. m.
	Minimum	Maximum	Average	Minimum	Maximum	Average	
1932 ...	113	800	240	28	173	69	2,905
1933 ...	14	122	31	6	98	21	3,544

We see from this table that in 1932 the maximum area per gallery system was 800 sq. cm., the minimum 113 sq. cm., and the average 240 sq. cm. The maximum production of beetles per gallery was 173, the minimum 28, and the average 69.

In the following year (1933) the maximum area per gallery system was 122 sq. cm., the minimum 14 sq. cm., and the average 31 sq. cm. In other words, the maximum area of 1933 was only a little more than the minimum of 1932, whereas the average area of 1933 was only 13 per cent. of the same for 1932. This was also reflected in the reduced production per gallery. The minimum figure of 6 is about 21 per cent. of the 1932 figure, the maximum, 98, a little more than 50 per cent., and the average figure, 21, about 30 per cent. of the corresponding figure for 1932.

Dr. Trägårdh attributes the decrease in production per gallery in 1933 to overcrowding brought about by the increased number of beetle galleries per square metre, but a more detailed analysis shows that overcrowding was not the most important factor, as the saturation point was not reached in 1933.

It can be estimated from the table that the number of galleries per square metre in 1933 was 169, as compared with 42 in 1932, although the increase in production was only 639, or the equivalent of an extra 10 galleries of the average production of 1932. It will be seen, therefore, that at the 1932 rate of production, 52 galleries would have produced 3,588 beetles as compared with 3,544 beetles from 169 galleries at the 1933 average rate of production.

The average area occupied per gallery system in 1932 was 240 sq. cm., which is greatly in excess of the actual requirements of the beetle, the number of galleries was 42 per sq. metre ; therefore, the galleries were distributed over the entire area.

In 1933 the average area occupied per gallery system was only 31 sq. cm. and the number of galleries was 169 ; the total area actually occupied by the gallery systems was, therefore, only 5,259 sq. cm., or 52·59 per cent. of the available breeding space. An equal distribution of the 169 galleries would give an available breeding space of 59 sq. cm. per gallery system.

In the New Forest during 1934, the present writer measured the whole of the *piniperda* galleries in a quantity of material of various sizes, chiefly poles under six inches diameter. The total number of galleries measured was 829 ; the measurements and numbers are shown below (fig. 1).

The total length of the 829 galleries was 4,014 inches ; therefore, the average length was 4·84 inches, or nearly 12·5 cm., although 4 inches gave the largest number.

An isolated egg gallery, 10 cm. in length, showed 120 larval tunnels, and this might reasonably be taken as representing the potential production of the average *piniperda* gallery. The total area occupied by the larval system of a gallery of this length was less than 14 cm. by 9 cm. (126 sq. cm.).

It will readily be seen that, provided that the galleries are evenly distributed, one square metre will accommodate 80 *piniperda* gallery systems, with an average area of 125 sq. cm. This is slightly above the maximum area of 122 cm. in 1933. The maximum production of 98 beetles per gallery in 1933 is not much below the figure which is taken as representing the potential production of a gallery of this size. The potential production may, therefore, be taken as 9,600 per square metre under optimum conditions. In the year 1932, with only 42 galleries per square metre, the potential production would be 5,040, but the actual production was only 2,905, or 57·64 per cent. of the possible. Even allowing for unequal distribution of the galleries, the difference of 42·36 per cent. cannot be accounted for by overcrowding, since the average area per gallery system was practically twice the amount required.

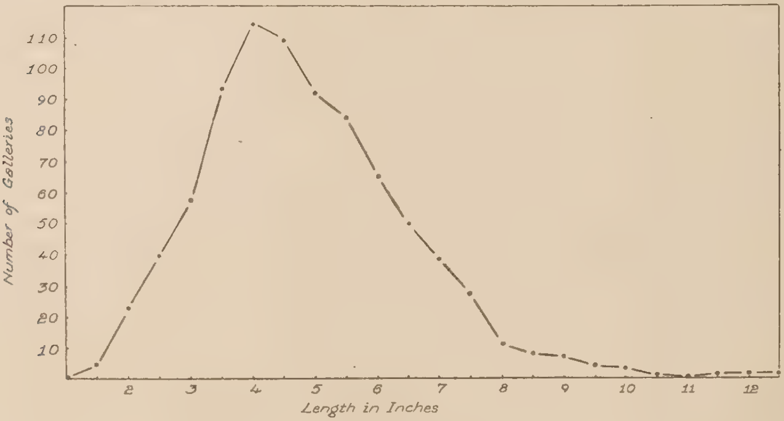

Fig. 1.

The following breeding experiment, carried out at Farnham House Laboratory during 1935, was designed to ascertain the rate of reproduction of *Myelophilus piniperda* in the absence of parasites and predators. Six small Scots pine billets were placed in separate breeding cages with about an inch of sterilised soil. A pair of *M. piniperda* was introduced into each cage and allowed to breed in the billets. In order to eliminate difference in size of breeding material as a factor influencing production, the billets were made uniform in size and it was considered that 9 inches in length by 2½ inches in diameter was the smallest size that could be safely used without risk of overcrowding becoming a factor of importance. The nature and thickness of the bark varied a little; billets 1 and 6 had very thin, smooth bark, while 2, 3, 4, and 5 had rather thicher and rougher bark, but no very rough, thick bark was used. The results are tabulated below (Table II).

The effects of the difference in bark is reflected in the length of egg gallery, the number of larval tunnels and the number of beetles that completed their development. The thin, smooth bark dried more quickly than the thicker bark, and mortality, due to desiccation, was more severe; this was particularly noticeable in the case of No. 6. The average length of the egg galleries was nearly 5 inches; the average number of larval tunnels was 113; and the average number of beetles that completed development was 66 for each pair of parent beetles. Very few, if any, of the eggs failed to produce larvae, and in two cases where eggs were laid at regular intervals along the galleries the number of eggs and young larvae was 26 per inch on one side of the gallery, almost exactly one egg per millimetre. In a gallery examined in the forest the number was 27 per inch. Eggs are seldom, however, laid at such regular intervals for much more than an inch and frequent gaps generally occur.

During the early stages the conditions in the breeding cages were very near ideal and the mortality of 58·4 per cent., which occurred during the later larval stage, was doubtless entirely due to desiccation, as a result of shortness in length, small diameter of the billets, and thinness of the bark. There was no sign of overcrowding and no mortality due to predators and parasites. The experiment will be repeated with larger billets and more favourable soil and humidity conditions.

TABLE II.

Number of billets	Length of egg-galleries	Maximum area of larval system	Number of larval tunnels	Number of beetles
1	3 inches	6 × 5=30 sq. ins.	72	56
2	7¼ inches	9 × 8=72 sq. ins.	189	110
3	4½ inches	7 × 6=42 sq. ins.	110	76
4	5½ inches	7 × 6=42 sq. ins.	127	72
5	7 inches	9 × 8=72 sq. ins.	145	67
6	2¼ inches	6 × 6=36 sq. ins.	35	15
Totals	29½ inches	294 sq. inches	678	396

The average number of beetles produced by each pair of parent beetles was 66, as compared with an average of 69 per gallery under optimum conditions in Dr. Trägårdh's figures for 1932. The average number of larvae in the above case was 113 per gallery system. If we take this figure as the potential rate of production in Sweden during 1932, it will be seen that the average mortality will be 39 per cent., and as there is no suggestion of overcrowding or desiccation in the 1932 material, it is reasonable to suppose that the mortality was largely due to the activities of parasites and predators. Taking the same potential rate of increase for the year 1933 in Sweden, it will be seen that the average rate of mortality would be 81·4 per cent.

Although unequal distribution of the galleries would undoubtedly cause considerable mortality through localised overcrowding, this could not possibly account for the whole of the 81·4 per cent., since only a little more than half of the available breeding space was utilised. Numerous observations made in this country by the present writer convinced him that the greater part of the reduction of production was due to destruction by predators, facilitated by the intermingling and linking up of the larval tunnels of the various gallery systems. Further reference will be made to this subject when dealing with predators.

Overcrowding certainly plays an important part in terminating bark-beetle outbreaks, by causing heavy mortality among the brood, and is probably one of the most important factors in restoring the balance of nature. We cannot, however, afford to allow infestations to develop until this factor automatically comes into operation, since our object is to prevent damage being done to the growing crop, and is not simply to terminate outbreaks and save the remnants of devastated crops from being completely destroyed. Nevertheless, it seems probable that the factor may be utilised to facilitate the control of bark-beetles. For example, a piece of smooth-barked Scots pine, 34 inches in length by 44 inches circumference, which had been cut off the end of a log and left lying in the forest because of a defect in the timber, was examined by the writer on 30th May 1933, in Buskett's Lawn Inclosure in the New Forest. The bark was removed and the following beetle galleries were counted :—

Species	No. of galleries
Myelophilus piniperda	4
Hylastes opacus	22
Hylastes attenuatus	8
Hylurgops palliatus	217
Ips laricis	43
Total number of galleries ...	294

The total area of bark was 10 square feet. It will be seen, therefore, that there were 29 galleries per square foot. A similar piece of timber was kept under observation, and before the larvae could complete their development the thin bark curled and shrivelled, resulting in the destruction of the entire brood. This line of investigation is being continued and further observations are being made with the object of finding out how to utilise the factor of overcrowding to the best advantage. It seems reasonable to assume that overcrowding can most easily be brought about by providing a supply of attractive breeding material of small diameter. The simplest way to do this is to leave a certain amount of material lying on the ground, when young plantations or natural pine stands are being thinned. The desired quantity of such material per acre can be ascertained only by experiment under various forest conditions.

Troshanin (1932) gives an account of an investigation carried out in the Tartar Republic (former Kazan Government) in the summer of 1928. The object of the investigation was to ascertain the extent to which lop and top left lying on the ground during the season following felling operations facilitates the increase of injurious pine beetles, and to demonstrate the danger of leaving this material in the vicinity of standing timber. In these circumstances the experiment cannot be regarded as being in any way biassed in favour of the arguments put forward by the present writer. The results of the investigation are, therefore, given in considerable detail.

A number of heaps of lop and top were formed. The heaps on the northern side of the area were exposed to sunlight and those on the southern side were in shade. One heap on the shaded side and two heaps on the sunny side of the area were divided into three sections—top, middle, and lower ; the branches in each section were classified according to their diameter. Sample branches were taken and the mother galleries and exit holes of the pine beetles were counted. The results are tabulated and are given below. The figures in Table III show that the maximum percentage of infestation occurs in the thicker branches.

Table IV shows the relationship which exists between the diameter of the branches and the choice of the bark-beetles for breeding purposes. The author points out that the production is maximum on the branches of greatest diameter, and that this type of material is the most dangerous. On the basis of these data, he states that the following " law " can be formulated : " The production of *Myelophilus minor* and *Ips acuminatus* increases with the increase of the diameter of the branches."

Table V gives the number of bark-beetles that populated the whole of the material. The author points out that the number is great and that there is reason to consider that the material constitutes a menace.

TABLE III.

Number of heaps	Position of heaps	Number of branches of each diameter per heap								
		1–3 cm.			4–6 cm.			7–9 cm.		
		Totals	Infested	Percentage of infestation	Totals	Infested	Percentage of infestation	Totals	Infested	Percentage of infestation
1	Southern side	324	74	22·84	264	109	21·28	134	64	47·76
2 and 3	Northern side	1,085	230	21·19	663	234	35·29	308	129	41·88
Total and average		1,409	304	21·57	927	343	37·00	442	193	43·66

TABLE IV.

Position of heaps	Number of exit-holes per average branch of each diameter											
	1–3 cm.				4–6 cm.				7–9 cm.			
	Myelophilus minor		*Ips acuminatus*		*Myelophilus minor*		*Ips acuminatus*		*Myelophilus minor*		*Ips acuminatus*	
	Mother galleries — Bark-beetle exit-holes	Average production per mother gallery	Mother galleries — Bark-beetle exit-holes	Average production per mother gallery	Mother galleries — Bark-beetle exit-holes	Average production per mother gallery	Mother galleries — Bark-beetle exit-holes	Average production per mother gallery	Mother galleries — Bark-beetle exit-holes	Average production per mother gallery	Mother galleries — Bark-beetle exit-holes	Average production per mother gallery
In shade (southern side)	7 — 47	6·7	26 — 42	1·6	16 — 132	8·2	33 — 212	6·4	101 — 678	6·7	30 — 294	9·8
Full light (northern side)	16 — 45	2·8	22 — 196	8·9	78 — 313	4·0	39 — 148	3·8	49 — 238	4·8	57 — 849	14·8
Total and average	23 — 92	4·0	48 — 238	4·9	94 — 445	4·6	72 — 360	5·0	150 — 916	6·8	87 — 1,143	13·0

TABLE V.

Position of heaps	Top sections			Middle sections			Lower sections			Total number		
	Myelophilus minor	*Ips acuminatus*	Total	*Myelophilus minor*	*Ips acuminatus*	Total	*Myelophilus minor*	*Ips acuminatus*	Total	*Myelophilus minor*	*Ips acuminatus*	Average per heap
Southern (shady side)	298 2,582	760 5,226	1,058 7,808	1,781 10,860	1,415 7,420	3,196 18,280	986 7,566	402 1,529	1,388 9,095	3,065 21,008	2,577 14,175	564 3,518
Northern (sunny side)	825 2,620	1,262 11,214	2,087 13,834	1,691 6,534	558 6,214	2,249 12,748	1,200 3,912	311 7,255	1,511 11,167	3,716 13,066	2,133 24,683	584 3,774
Northern (sunny side)	192 1,416	480 3,168	672 4,584	598 2,770	648 2,113	1,246 4,883	360 1,555	410 2,035	770 3,590	1,150 5,741	1,538 7,316	268 1,305

Note. 1. The top figures give the number of mother-galleries ; the bottom figures the number of exit-holes.

Note 2. The galleries of *Ips bidentatus* were ignored, as this species is of secondary importance and occurred in small numbers only.

Table VI shows the degree of infestation of the heaps per cubic metre depending upon the position ; *i.e.*, whether exposed to full light or shaded. It shows that the number of beetles is greater on the shaded side of the felled area. This number is largely due to the predominance of *Myelophilus minor*.

TABLE VI.

Position of heaps	Average number of bark-beetles per cubic metre		
	Myelophilus minor	*Ips acuminatus*	Total
Southern (shady side)	261 galleries 1,786 exit-holes	220 galleries 1,205 exit-holes	481 galleries 2,991 exit-holes
Northern (sunny side)	164 galleries 633 exit-holes	124 galleries 1,077 exit-holes	288 galleries 1,710 exit-holes

Table VII shows the average production per mother gallery for each species of bark-beetle in each class of material.

TABLE VII.

Position of heaps	Sections of heaps						Average production per mother gallery	
	Top		Middle		Lower			
	Production per mother gallery							
	Myelophilus minor	*Ips acuminatus*	*Myelophilus minor*	*Ips acuminatus*	*Myelophilus minor*	*Ips acuminatus*	*Myelophilus minor*	*Ips acuminatus*
Southern (shady)	8·7	6·9	6·1	5·2	7·7	3·8	6·8	5·5
Northern (sunny)	4·0	8·3	4·1	6·9	3·5	12·9	3·9	8·7

In the case of *Myelophilus minor*, the maximum production, 8·7 per gallery, occurs in the top layers of the heaps on the shady side and the average is 6·8 per gallery, as compared with 3·9 per gallery in the heaps on the sunny side.

On the other hand, in the case of *Ips acuminatus*, the maximum production, 12·9 per gallery, occurs in the lower layers of the heaps on the sunny side, and the average production in these heaps is 8·7 per gallery, as compared with 5·5 per gallery on the shady side. On the basis of the figures shown in Table III, which gives the total number for the whole of the material, the average production is 6 beetles per gallery.

The author points out that one cubic metre (see Table VI) contains 481 mother galleries and produced 2,991 beetles, and states that this number represents from one-fifth to one-third of the maximum number of bark-beetles that can breed on a tree of 40 centimetres in diameter, and that 3 to 5 cubic metres of material would be sufficient to infest fully a tree of that size. The author concludes that the material constitutes a menace, but it is difficult to understand how he arrives at this conclusion. The production of 6 beetles per gallery gives only a net increase of 4 beetles per gallery. When we consider the risk of casualties from birds and other predators, and the death rate due to climatic reasons, this is a narrow margin with which to carry over the species to the next breeding season, and does not allow the beetles much chance of maintaining the level of the population from year to year. Moreover, the figures given in the table show the total number of exit-holes, and as no mention is made of parasites, it seems probable that some of the exit-holes are those of Hymenopterous parasites, in which case the production of bark-beetles per gallery will be even less than the figures indicate. An outstanding feature of the experiment is the fact that the greatest production per gallery takes place in the material of the greatest diameter. This fact is particularly stressed by the author, and it is on this basis that he formulates his " law." Conversely, the smaller the diameter of the breeding material, the less is the risk of an increase in the population. That being the case, it is reasonable to assume that in the absence of the material under 9 cm. diameter, the bark-beetles would doubtless have attacked the suppressed trees in the nearest forest stand. In that event, according to Troshanin's " law," the result would have been a much greater increase in the bark-beetle population. It will be seen, therefore, that the actual results of the experiment indicate that the presence of this small-diameter material is a distinct advantage and not a menace, and that the evidence points to conclusions directly opposite to those arrived at by Troshanin, and produced results exactly the reverse of those for which the experiment was designed, namely, to demonstrate the danger of leaving this material in the vicinity of standing timber.

In the case of breeding material of very small diameter, the production per mother gallery is often extremely low. Trägårdh (1921) gives an analysis of 12 stems under 2·5 cm. diameter, and shows that of 460 eggs laid, only 78·2 per cent. produced larvae and only 0·43 per cent. developed into mature insects. The details are given in Table VIII.

Dr. Trägårdh points out that the length of the mother gallery in this class of material rarely exceeds 5 cm., and seldom reaches 8·5 cm. The average length is 5·4 cm., as compared with an average of 10 to 12 cm. in material of much greater dimensions. The average number of eggs was 38·3, the number of larvae 30, and the number of mature insects 0·166 per mother gallery. The biotic potential was therefore 38·3, but on account of overcrowding, desiccation and other factors, it sank to less than 0·44 per cent. of this number. It will be seen from the above that breeding material of very small diameter acts as a death-trap. Although no mention is made of predators as contributory factors in the decimation of the broods in the above case, there appears to be some evidence of their activity ; for example, in the second column only 4 larval tunnels arose from 22 eggs ; in the third, 11 larval tunnels from 29 eggs ; in the ninth, 20 larval tunnels from 40 eggs. In the 5th, 6th and 7th, the number of larval tunnels corresponds exactly with the number of egg-pockets, but although in these cases the eggs evidently escaped the attack of predators, it does not preclude the possibility of the subsequent destruction of the larvae by predators. In any case, the small diameter of the material is undoubtedly a prime factor in facilitating overcrowding and the destruction of the broods.

The rate of growth of the crop is of great importance in facilitating or limiting the operation of overcrowding as a factor in the automatic control of bark-beetles in standing pine forests. An adequate and well-sustained supply of suitable breeding material is the most important requirement of an increasing bark-beetle population, and to meet this requirement a larger supply of suitable breeding material is required from year to year. Maximum opportunities for rapid increase occur when the available material is in excess of the requirements. When the supply of suitable breeding material falls below the necessary minimum requirement, overcrowding inevitably takes place and may result in heavy mortality among the brood and may even result in a temporary decrease in the population. In slow-growing pine stands the increase in available supplies of suitable breeding material is very limited and

TABLE VIII.

Diameter at the base	2 cm.	2·5 cm.	2 cm.	2·4 cm.	2·4 cm.	2·2 cm.	2·2 cm.	2·2 cm.	2 cm.	2·5 cm.	2 cm.	2·3 cm.
Length of mother-gallery ...	3·5 cm.	4 cm.	4 cm.	4·4 cm.	4·5 cm.	4·5 cm.	5 cm.	5 cm.	5·5 cm.	7·5 cm.	8·5 cm.	8·5 cm.
Number of egg pockets	32	22	29	23	20	31	30	39	40	53	64	78
Number of larval tunnels ...	28	4	11	15	20	31	30	33	20	47	50	70
Number of pupal chambers ...	0	0	0	0	0	0	0	0	0	0	0	2

overcrowding among the pine-beetle population is greatly facilitated. On the other hand, in rapidly growing crops, larger supplies of suitable breeding material are available and the factor of overcrowding is consequently limited in operation.

3. Parasites and Predators.

The indiscriminate use of the term "parasite" and "predator" as interchangeable causes considerable confusion. Unfortunately, a number of writers on entomological subjects still persist in using the terms in this loose, slipshod manner. It is not easy to give a satisfactory, clear-cut definition of the terms in a few words, but for the present purpose, the use of the term "parasite" is confined to organisms which complete their development at the expense of a single host individual of any species, irrespective of whether that host is attacked internally or externally. In the case of insect parasites the destruction of the host is generally accomplished only by the larvae, although some adult parasites actually feed on the juices of host larvae without, however, destroying the tissues. The use of the term "predator" is limited to species which attack and devour a number of hosts in succession, killing and eating each host as and when required. In the case of predators, the hosts are generally destroyed by both the larvae and the adults. For convenience, the two groups will be dealt with separately.

(i). *Parasites.*

The bark-beetle parasites may be described as follows: (*a*) Disease-producing organisms; (*b*) Nematode worms; (*c*) Hymenoptera.

(*a*) *Disease-producing organisms.*

There is no evidence to show that disease-producing organisms play any part in the control of *Myelophilus*. In any case these organisms cannot be regarded as important even if they do cause an epidemic when the pest has reached its maximum abundance. The object of our control measures must always be to prevent the bark-beetle population approaching that stage of density.

(*b*) *Nematode worms.*

Although Nematode worms are of frequent occurrence as parasites of bark-beetles they cannot be regarded as being of great importance as controlling agents. Under exceptionally favourable conditions for their existence they may be extremely numerous, and sometimes large numbers of bark-beetles may be infested, while at other times it is possible to examine batches of beetles without finding any of the Nematodes present. Considerable difference of opinion exists as to the extent of their effects on the host. Fuchs (1914) states that the effects of parasitic Nematodes upon the bark-beetle is to lower the general activity and, in particular, its egg-laying capacity, parasitised beetles laying about half the number of eggs laid by healthy individuals. Greze (1926) studied the effects of parasitic Nematodes on the reproduction of *Myelophilus minor*, but it was found that their presence in the host did not affect its reproductive organs unless the parasites occurred in large numbers. Though over 23 per cent. of the beetles were infested with Nematodes, only 2 per cent. were seriously affected. Oldham (1930) studied a Nematode parasite in the elm bark-beetles, *Scolytus destructor*, Ol., and *S. multistriatus*, Marsh. About 60 per cent. of the beetles examined contained Nematodes within the body cavity, the effects being to reduce the reproductive organs of the host; 24 per cent. of the beetles were classified as sterile.

The state of development of the reproductive organs of bark-beetles varies considerably during different stages, and although the ovaries appear shrivelled in sexually immature adults, and again after egg-laying, they are capable of recuperation after a period of feeding. It appears, therefore, that the difference in the results obtained in the examinations mentioned above may have been influenced by the state of the insects at the time the observations were made. The question is, however, of relatively little importance as it is impracticable to utilise Nematode worms as factors in control measures, and it seems probable that their usefulness as parasites of bark-beetles will be neutralised by their effects upon the Coleopterous predators.

(*c*) *Hymenoptera.*

In the past the study of the Hymenopterous parasites of pine bark-beetles appears to have been completely neglected in Britain. During the course of the present investigation the following species have been reared from pine-beetle material collected in the forest :—

BRACONIDAE : *Coeloides abdominalis*, Zett., *Dendrosoter middendorfi*, Ratz., *D. protuberans*, Nees., *D. hartigi*, Ratz., *Calyptus atricornis*, Ratz.

EURYTOMIDAE : *Eurytoma auricoma*, Mayr.

EUPELMIDAE : *Eupelmus urozonus*, Dalm.

PTEROMALIDAE : *Roptrocerus xylophagorum*, Ratz., *Rhopalicus tutela*, Walk. (=*suspensus*, Ratz.), *R. brevicornis*, Thoms., *Pteromalus bidentis*, Ratz.

This list includes all the species that have been identified, but is not complete, as certain species, of which only individual specimens were obtained, have not yet been determined ; in other cases adult specimens were not successfully reared, and it is anticipated that other species will be found as the scope of the work is extended.

Of the above species, nine were found as parasites of *Myelophilus piniperda*, L., and in most cases were also associated with *Hylurgops palliatus*, Gyll., but the latter species is of little economic importance.

The Pteromalid, *Rhopalicus tutela*, Walk., is by far the most important *Myelophilus* parasite in Britain, and has been most frequently recorded as a parasite of this species on the Continent, where it has been recorded from eight other bark-beetles under the name *Pteromalus suspensus*, Ratz. Dr. Ferrière, of the Imperial Institute of Entomology, who determined the above species, considers that one or two other names which have appeared in the Continental literature probably refer to the same insect. This species is very abundant and is widely distributed. It was present in every locality visited in England and Scotland. In the New Forest during the winter of 1933–34, the whole of the material in one of the sample plots, a tenth of an acre in extent, in a thinning experiment, was examined to take a sample census of the parasite population. The number of bark-beetle parasite larvae was found to be 64,600 per acre ; of these more than 99 per cent. were *Rhopalicus tutela.* In addition to the above, one generation of parasites had emerged from the material during the summer prior to the emergence of the bark-beetles. No Braconid parasites were found in this material, their absence being probably due to the fact that all the poles were lying flat on the ground ; Braconid parasites appear to prefer standing trees or material which is not very near the ground, but Chalcids seem to be indifferent and are found in all situations above ground-level. *Rhopalicus* readily attacks other species of pine-beetles, and was also frequently found as a parasite of *Pissodes notatus.* An interesting point in this connection is that when *Pissodes* was the host, the *Rhopalicus* larva was always found to be less than normal in size, even when the host larva had been quite double the size of a full-grown *Myelophilus* larva. In some cases the parasite larva was only slightly larger than the head-capsule of the devoured host. *Rhopalicus* does not appear to have been recorded as a parasite of *Pissodes* in Europe, but has been recorded as a parasite of *Pissodes strobi*, Peck., in the United States of America.

The Braconids, *Coeloides abdominalis*, Zett., and *Dendrosoter middendorfi*, Ratz., were most numerous in dry districts, such as Woburn and Bagshot, but were also found in the New Forest. Both species were most frequently found in the bark of standing trees.

Calyptus atricornis, Ratz., was found only as an occasional parasite of *Myelophilus*, but this species is a very efficient parasite of *Pissodes notatus* and is numerous in the New Forest.

Roptrocerus xylophagorum, Ratz., and *Rhopalicus brevicornis*, Thoms., have not been found to be very numerous in any locality, but both species were found as parasites of *Myelophilus*. The former probably occurs more frequently as a parasite of spruce bark-beetles, judging by the records in Continental literature ; but so far the writer has not looked for it on other than pine bark-beetle material.

Eupelmus urozonus, Dalm., appears to be comparatively scarce as a parasite of pine-beetles and is probably a hyperparasite, but this point has not yet been established in the present case.

Eurytoma auricoma, Mayr, is a hyperparasite of *Rhopalicus tutela*, but has not been found to be present in excess of 2 per cent. It is not yet definitely known whether it is in some cases primary.

The other three parasites have not yet been found attacking *Myelophilus*. *Dendrosoter protuberans*, Nees, is probably a recent introduction to Britain. It was found by the present writer at Bagshot in 1931, as a parasite of *Ips suturalis*, Gyll., and had not previously been recorded in Britain, but has frequently been recorded on the Continent. Most of the latter records are from hosts feeding in the bark of hardwoods, and the fact that these host trees include maple and fruit trees suggests that *D. protuberans* prefers a warm climate. Incidentally, the host, *Ips suturalis*, has only been previously recorded from four localities in Britain. Each of the records suggests that the insect concerned was probably of recent importation. One of the records was actually from pitwood imported from France. It appears likely that both species were introduced into Britain in that way. However, they seem to have become established, as both have since been recorded from Windsor Forest.

Dendrosoter hartigi, Ratz., has been found to be extremely efficient as a parasite of *Pityogenes bidentatus*, Herbst. In some cases every *bidentatus* larva in the brood has been parasitised. The species is very widely distributed in Britain. The sexes are quite different in appearance, and each sex was originally regarded as representing a separate species belonging to different genera and were given different names, the female being *Dendrosoter hartigi*, Ratz., and the male *Coenopachys hartigi*, Ratz.

Pteromalus bidentis, Ratz., is also a very abundant parasite of *Pityogenes bidentatus*. The writer has also found this species attacking *Cryphalus abietis*, Ratz., and *Pityophthorus pubescens*, Marsh. This parasite seems to be even more widely distributed than the preceding species and is probably the insect referred to by Munro (1926) as " Proctotrypid wasps," the larvae of which, he states, " are to be found in the pupal beds of the *Pityogenes* larvae in most brood galleries." No Proctotrypid parasite of pine bark-beetles has so far been found by the present writer, and no records appear in the Continental literature.

Although parasites must be recognised as very important factors in the control of bark-beetles, they are of relatively minor importance as compared with the predators. The work of the parasites is more conspicuous because of the fact that each larva or pupa is accompanied by the head-capsule of the host larva destroyed. This facilitates the identification of the parasite with the work it has accomplished. In the case of the generation of parasites which overwinter in the larval stage, the head-capsule of the host and the parasite larva are to be found lying together during the whole of the autumn and winter. In the case of the predators the work of destruction is carried out more unobtrusively, and no indication, even of a temporary character, is left by which the death of the host can be definitely associated with any particular individual predator. The value of the parasites must not, however, be underestimated. It should be remembered that every parasite larva represents a host larva that has escaped destruction by predators and the effects of overcrowding, and, as Schimitschek (1931) has pointed out, parasites reduce the abundance of Scolytids to the residual minimum.

(ii). *Predators.*

The principal predators concerned in the destruction of pine bark-beetles will be referred to in the following order :—(*a*) Coleoptera, (*b*) Neuroptera, (*c*) Diptera, (*d*) Birds, etc.

(*a*) *Coleoptera.*

Although certain species of beetles have for many years been recognised as associated with the destruction of the broods of bark-beetles, no steps have been taken in Britain in the past to ascertain the extent of this destruction or how the predatory proclivities of these insects can be utilised to the best advantage in the control of bark-beetles. A certain amount of work has been done in this direction in Europe and America, but the work has not been attended with much success, for reasons which will be referred to in dealing with the various species concerned. The following is a list of the species which have been found associated with pine bark-beetles during the course of this work ; the list will probably be extended as the work progresses.

STAPHYLINIDAE : *Phloeopora reptans*, Gr., *Homalota aequata*, Er., *Leptusa haemorrhoidalis*, Heer., *Mycetoporus lepidus*, Gr., *Othius melanocephalus*, Grav., *Stenus atratulus*, Er., *Homalium pusillum*, Gr., *H. punctipenne*, Th., *Prognatha quadricornis*, Kirb.

NITIDULIDAE : *Glischrochilus quadripustulata*, L., *G. quadripunctata*, Hbst., *Epuraea pusilla*, Ill., *E. obsoleta*, F., *Pityophagus ferrugineus*, F., *Rhizophagus depressus*, F., *R. ferrugineus*, Pk., *R. dispar*, Pk., *R. bipustulatus*, F.

ELATERIDAE : *Elater rufipennis*, Steph., *Melanotus rufipes*, Hbst., *M. castanipes*, Pk.

CLERIDAE : *Thanasimus formicarius*, L.

TENEBRIONIDAE : *Hypophloeus linearis*, F., *H. fraxini*, Kug., *Helops striatus*, Fourc.

PYTHIDAE : *Rhinosimus planirostris*, F., *R. ruficollis*, L.

It is not suggested that all the above species are of economic importance. On the contrary, the writer is of the opinion that many of them are of no importance. They have been included in the list merely because they are frequently found associated with the bark-beetle broods. For example, few, if any, of the STAPHYLINIDAE can be regarded as being of economic importance, as they are seldom found in the bark-beetle galleries until the bark-beetle larvae are in an advanced stage of development. The majority of the STAPHYLINIDAE are most frequently found associated with *Hylurgops palliatus*, particularly when the latter is breeding in spruce bark.

The NITIDULIDAE are the most important group of bark-beetle predators. The two species of *Glischrochilus* occur most frequently in the North of England and in Scotland. The writer has not yet had the opportunity to study their habits in detail, and their economic status is still in doubt.

Little attention has been paid to the genus *Epuraea*, and it is anticipated that other species will be found to be predators of pine beetles. *Epuraea* larvae are very common in the galleries and have frequently been observed destroying the brood. *Pityophagus ferrugineus* is a very efficient predator and is very numerous in the South of England. It is found in *piniperda* galleries in the stumps of trees and in logs on the ground. It is of great importance as a predator of *Hylastes ater* and the pine weevil, *Hylobius*.

The various species of *Rhizophagus* are by far the most important enemies of bark-beetles and their value can scarcely be over-estimated. They are extremely numerous and their efficiency as factors in the destruction of bark-beetle eggs and larvae is definitely established. *Rhizophagus ferrugineus* appears to be most numerous and most widely distributed enemy of *M. piniperda*, and has been found in almost every locality visited, in both England and Scotland. It is a prolific species ; in one experiment a single female destroyed 79 *Hylastes* eggs, and laid 39 eggs. *Hylastes* eggs were used in this experiment because it was carried out late in the season and *piniperda* eggs were not so easily obtained. *Hylastes* will breed during almost every part of the year. *Rhizophagus dispar* does not appear to be so numerous in the South of England as in the North of England and in Scotland, where it is very plentiful, and rivals *R. ferrugineus*. It was found to be the commonest species in Perthshire.

Rhizophagus depressus is widely distributed, but it is not so numerous as either of the above species. Both *R. ferrugineus* and *R. depressus* are great enemies of *Hylastes ater*.

Rhizophagus bipustulatus is often found attacking *M. piniperda* broods, but appears to be more frequently associated with *Hylurgops palliatus*, particularly when the latter is breeding in spruce. *R. bipustulatus* was also found to be very numerous in the galleries of *Hylastes cunicularius*, Er. Several other species of *Rhizophagus* have been recorded as predators of pine bark-beetles on the Continent, and, as they are also British species, it seems probable that they will be found to supplement the above species in this country. An important point about the species of *Rhizophagus* is that their destruction is almost entirely confined to the eggs and young larvae of the pine beetles. The larvae of *Rhizophagus* complete their development early and leave the bark to pupate in the soil, and unlike many of the other predators they cause comparatively little destruction to the parasite larvae.

Several species of Elaterid larvae are found as predators of bark-beetle larvae and pupae. The three species above have been reared to the adult stage, but others remain to be added to the list. The ELATERIDAE cannot, however, be regarded as very useful allies, as they take a long time to complete their development and cause great destruction among the parasite larvae and pupae after the bark-beetles have completed their development and have emerged from the bark. Fortunately, the Elaterids are not very numerous and do not appear to be very prolific. They are, however, of considerable importance and are being studied with a view to the elimination of conditions which favour their increase.

The Clerid, *Thanasimus formicarius*, L., is the most conspicuous of the bark-beetle predators and has attracted more attention than any of the other species. *Thanasimus* is very voracious in both larval and adult stages. The adult beetle readily destroyed adult bark-beetles even when confined in glass tubes in the hand of the observer, but they just as readily devour *Rhizophagus* adults. The larvae of *Thanasimus* feed on bark-beetle larvae and pupae and destroy large numbers. They are, however, equally destructive to the larvae of *Rhizophagus* and *Epuraea* and when present, undoubtedly cancel the beneficial effects of their work by causing the wholesale destruction of the other predators, thereby reducing the level of the predator population. Moreover, they continue to feed in the bark after the remnants of the bark-beetle brood have completed their development and emerged. By the end of July most of the *piniperda* have left the bark, but the parasite larvae remain throughout the autumn and winter, then pupate and emerge as adults during the following spring. At the time when the *piniperda* emerge in July, the *Thanasimus* larvae are only about half-grown. They continue their development, subsisting almost entirely on the helpless parasite larvae throughout the autumn and if the weather is mild they continue to feed well on into the winter. If the weather is severe they excavate chambers in the bark, in which they hibernate until the spring, when they commence to feed again and complete their development. If the available food supply is scarce they readily devour each other and very few survive.

This cannibalistic tendency probably accounts to some extent for the comparative scarcity of the adults. When the bark is thin the whole of the parasite larvae lie between the bark and the wood, and are easily accessible. When the bark is thick, the bark-beetle larvae escape parasitism until they burrow into the bark and form their pupal chambers. In this position many become parasitised and the parasite larvae are isolated and protected from the majority of the predators. This does not act as a deterrent to *Thanasimus* larvae ; the latter burrow into the bark and devour the parasite larvae. In cases where *Thanasimus* larvae are fairly numerous, practically the whole of the other predator larvae and parasite larvae may be destroyed, and although *Rhizophagus* may have been responsible for the destruction of the greater part of the bark-beetle brood, *Thanasimus* larvae may be the only predators present when the material is examined.

Much difference of opinion exists as to the value of *Thanasimus* as a predator. Neckleba (1929) states that careful observations in Czechoslovakia of the larvae of *Thanasimus* failed to disclose any useful action on its part. On the other hand, Pfeffer (1934) states that in Czechoslovakia the bark-beetles were preyed on by numerous Coleoptera, of which the Clerid, *Thanasimus formicarius*, was the most important and widespread. Butovitsch (1925) refers to *T. formicarius* as one of the most dangerous enemies of *Myelophilus piniperda*.

The present writer considers *Thanasimus* to be more harmful than useful, on account of the destruction it causes to useful predator and parasite larvae and regards the insect as the equivalent of the hyperparasites among Hymenoptera. This species was selected by Hopkins for introduction into the United States from Europe in 1892–3, to control *Dendroctonus* outbreaks. The failure of the experiment has since been frequently cited by critics of biological control, as an example of the futility of the method.

The habits of the insect are being studied with a view to formulating measures for limiting its activities in pine areas, if found desirable and necessary. A possible redeeming feature will be referred to when discussing Diptera.

The TENEBRIONIDAE are of little importance as predators of *Myelophilus piniperda*, but are occasionally found in the galleries. *Hypophloeus linearis* is, however, a very important predator of *Pityogenes bidentatus*. It is very common and widely distributed. *Hypophloeus fraxini*, on the other hand, is a very rare insect. It was found at Bagshot in 1931 in the gallery of *Ips suturalis* and had previously been recorded as occurring in the galleries of *Ips sexdentatus* in imported mining timber.

Although extremely common, the economic status of *Helops striatus* is not definitely known. It is included in the above list because of the frequency with which it is found associated with bark-beetles and weevils. The writer has not seen it attack the larvae of bark-beetles, but has found it feeding on parasites of both bark-beetles and *Hylobius*. It seems probable, therefore, that the species is in the same category as the ELATERIDAE.

Of the PYTHIDAE, two species have occasionally been found in *piniperda* galleries, but more frequently they are found associated with *Hylurgops palliatus*. Their economic status is not yet known.

In addition to the species mentioned in the above list, occasional specimens of several other species have from time to time been found in bark-beetle galleries ; among these are a few of the smaller species of CARABIDAE, but it is not considered that they are normally associated with the destruction of bark-beetle larvae.

Although not predators, two other species of beetles deserve mention as being beneficial under certain conditions. These are the Cerambycids, *Rhagium bifasciatum*, F., and *Asemum striatum*, L. ; their usefulness lies in the destruction of the cambium layer, thus rendering the bark of tree stumps unsuitable for the breeding purposes of bark-beetles. They are particularly useful as controlling factors in the case of *Hylastes ater* and the pine weevil, *Hylobius*.

(*b*) *Neuroptera.*

The larvae of a species of Neuroptera, *Raphidia notata*, F., is occasionally found associated with the brood of *Myelophilus piniperda* in the New Forest. The insect is very voracious and probably destroys parasite and predator larvae as readily as bark-beetle larvae. It is not, however, of very frequent occurrence and has not yet received much attention.

(*c*) *Diptera.*

As in the case of the Hymenoptera, little attention has hitherto been paid to the Diptera associated with bark-beetles in Britain. A large number of the species found breeding under loose bark are of no economic importance. A few species are, however, definitely associated with bark-beetles as predators. Of these, the following species have been reared during the course of the present work :—

STRATIOMYIIDAE : *Pachygaster minutissima*, Zett.

DOLICHOPODIDAE : *Medeterus obscurus*, Zett.

ANTHOMYIIDAE : *Phaonia goberti*, Mik.

LONCHAEIDAE : *Lonchaea tarsata*, Fln., *L. deutschi*, Zett.

In addition, several species have been found but have not yet been successfully reared in a state fit for determination. The list is not, therefore, complete and will doubtless be extended. Of the five species mentioned, only the last four are of importance. All four species are common, but the first species is rare. *Medeterus obscurus* is of particular interest. This species is particularly abundant and is one of the most numerous of the insects associated with the broods of *Myelophilus piniperda*. Nevertheless, when specimens were sent to the Imperial Institute of Entomology for determination in 1931, the species was stated to be new to Britain.

Although listed as predators of bark-beetles, the above species are of far greater importance as destroyers of the parasite larvae. They seldom occur until the bark-beetle brood is in an advanced stage of development, and although they make their appearance in time to destroy a few bark-beetle larvae and pupae, they are most in evidence during the period following the emergence of the bark-beetles and are to be found in large numbers throughout the autumn, winter, and early spring, during which period no *piniperda* larvae or pupae are present, and the pupal chambers contain only the Hymenopterous parasite larvae, which are devastated by the larvae of the Diptera.

It has been mentioned that the larvae of *Thanasimus formicarius* are also present in *piniperda* brood-galleries during the autumn and winter. An effort will be made to ascertain whether, and to what extent, the *Thanasimus* larvae feed on the Dipterous larvae. If satisfactory evidence can be collected, it is possible that a method of utilising *Thanasimus* may be evolved. The only parasite of the Diptera found to date is a single specimen of the Cynipid, *Kleditoma elegans*, Cam.

The biology and economic status of the most important parasites and predators will be dealt with in due course.

(*d*) *Birds.*

The economic status of birds in relation to forest insects has received considerable attention from time to time and much conflicting evidence has been produced ; for example, various authorities have expressed directly opposite views as to the status of woodpeckers, and it is extremely difficult to arrive at any definite conclusion as to the extent to which these birds can be regarded as beneficial. The writer considers that most of the evidence brought forward to show that woodpeckers cause serious damage to growing trees is without substantial foundation. On the other hand, the evidence presented to show that they are very beneficial requires to be examined very carefully. The plan generally adopted in attempts to assess the economic status of birds is to make an analysis of the contents of the stomach of a large number of each species during various parts of the year. The results are tabulated to show the percentage of each type of food and may be expressed in terms of bulk, or in numbers of individual species. Very often the writers classify the insects according to the Orders to which they belong and state that a given number or certain percentage of injurious or beneficial insects are present ; but since opinions often differ as to whether certain species are injurious or beneficial, the figures are liable to considerable latitude of interpretation ; for example, *Rhagium bifasciatum* and *Asemum striatum* figure largely in the lists of injurious species, but it has been shown that under certain conditions these species may be regarded as very beneficial.

As a keen amateur ornithologist, the writer is anxious to recognise and acknowledge any beneficial work that can be placed to the credit of birds and he has neglected no opportunity to make careful observations as to their activities in connection with bark-beetles. He is, however, reluctantly compelled to confess that little evidence has been observed as to their usefulness in the destruction of bark-beetle broods. Occasionally, in the case of blown trees lying at an angle, evidence of the attack of birds on the brood galleries has been observed, but the work has been on a very limited scale and was of such a character as to suggest that the species concerned were not normally associated with the habit of attacking the bark while the tree is in a vertical position, but required a convenient perch to enable them to secure a good foothold, while breaking away the bark with their powerful beaks.

An examination of the work of woodpeckers on a dead tree will readily convince the observer that a very large expenditure of apparently futile effort often takes place. A large proportion of the work consists of merely enlarging the exit-holes made by *Rhagium* and *Sirex*. Most of this work on dead trees takes place during the winter, at which time the exit holes are populated by hibernating insects, etc., and the operations are doubtless rewarded by the capture of insects, spiders, and woodlice, which have taken temporary shelter in the holes.

During the winter *Myelophilus* larvae and pupae are not normally present in the bark, but large numbers of parasite larvae are present. It will be seen, therefore, that the activities of woodpeckers may result in the destruction of the parasite larvae. The destruction may be brought about directly by the birds eating the larvae, or indirectly, by pieces of bark containing the larvae becoming detached and falling to the ground. A critical analysis of the stomach content would, of course, disclose the presence of the parasite larvae if the analysis were made immediately after the larvae were eaten, but even a specialist in Hymenoptera would have difficulty in determining the identity of the larvae. After two hours had elapsed no trace of the larvae would be found. On the other hand, the hard chitinous parts of beetles may be present in the stomach after four hours have elapsed.

It seems probable, therefore, that many records of woodpeckers destroying bark-beetle broods are, in fact, cases of the destruction of parasite larvae. The position is, of course, somewhat different in Canada and the United States, where certain species of bark-beetles may be found in the larval state in the bark in winter.

Rhizophagus adults are often extremely numerous under the bark of dead trees in winter and it is reasonable to suppose that many of them fall victims to birds when the bark is dislodged. The writer has found over a hundred *Rhizophagus* adults under a piece of bark less than six inches square. During the flight period, when a bark-beetle infestation is severe, birds undoubtedly are responsible for the destruction of very large numbers of adult beetles in woods bordering on agricultural lands. It must, however, be recognised that insectivorous birds are not very numerous in coniferous forests, and when they do occur, are most numerous in the immediate vicinity of human habitations. When coniferous forests are extensive and remote from human dwellings, the insectivorous birds are comparatively scarce. In fact some of the small insectivorous birds are undesirable in pine forests, on account of the enormous number of COCCINELLIDAE they destroy, and an investigation would probably show that *Leucopis* and Hemerobiid larvae suffer equally severely.

The encouragement and artificial increase in the bird population in large pine forests in remote districts by means of nesting boxes is impracticable and would, in any case, be useless as a measure for the control of bark-beetles, as the broods are hidden from the birds by the bark in which the beetles are breeding and are not accessible, as in the case with sawfly larvae and other leaf-eating insects.

It will be seen from the above remarks that birds cannot be regarded as important factors in the control of bark-beetles, and although it is possible to ascertain by means of an exhaustive study of the stomach contents what proportion of any bird's diet consists of any given species of insect, it is quite impossible to arrive at any definite conclusion as to the percentage of the bark-beetle population which is or might be destroyed by birds. Experiments designed for this purpose are bound to give misleading results, and any figures which are put forward as representing the percentage of bark-beetle populations destroyed by birds must be regarded with suspicion.

4. Effects of Competition between different Species of Bark-beetles.

Whether we study the forest as a whole or select a single suppressed or dying tree, we find that there is a regular succession in the order of attack by the various species, and certain species show a preference for particular parts of the tree. In Britain *Hylobius* and *Hylastes* attack the roots and *Myelophilus* attacks the stem. This attack takes place while the tissues are still alive and the tree is rapidly reduced to a state in which it is suitable for the breeding purposes of the secondary insects. *Pissodes*, *Hylurgops*, *Ips laricis* in the south, and *Ips acuminatus* in the north, attack the bark of the stem. *Pityogenes bidentatus* attacks the bark of the upper part of the stem and the branches, and is followed by *Pityophthorus pubescens*, *Cryphalus abietis* and others. The subject has been dealt with by Trägårdh (1921 and 1927) and Golovyanko (1926). While certain species will mix together indiscriminately and infest the bark to such an extent as to cause mutual destruction through overcrowding, other species, while readily overcrowding the bark in company with other specimens of their own species, appear to avoid breeding in contact with other closely allied species. This is particularly the case with *M. piniperda* and *M. minor*. The reason may be that they prefer slightly different breeding conditions, or because of the difference in their gallery formation, *M. piniperda* forming its galleries parallel with the main axis of the stem, while *M. minor* forms galleries running in a transverse direction. It is clear that in the event of the two species breeding mixed together, both species would be greatly inconvenienced. The former writer has shown that when *M. minor* is present, the attack of *M. piniperda* on a pine 46 ft. high, ceases at 20 ft.; but when the former is absent, the latter will extend its attack on a tree of the same size up to 36 ft. *M. piniperda* undoubtedly prefers the thicker-barked portion of the stem, while *M. minor* definitely prefers the upper thin-barked portion. Ritchie (1917) gives particulars of several trees which he examined. In the case of a thirty-year-old suppressed tree, in which both species of *Myelophilus* were breeding, *M. piniperda* galleries were plentiful in the lower 4 ft. of the stem without a trace of *M. minor*; whereas from this height upwards to the crown, *M. minor* galleries were very plentiful. In another similar stem there was no trace of *M. piniperda* brood-galleries, and *M. minor* galleries commenced at 1 ft. above the surface of the ground and continued upwards to the crown. In another stem of similar age, which was comparatively thin-barked throughout its whole length, *M. minor* galleries were very plentiful from the surface of the ground to the crown of the tree. He considers that *M. minor* seeks a better quality of food material than *M. piniperda*. This indicates that the former will more readily attack vigorously-growing trees. This conclusion is substantiated by Wolff (1924), who says that, contrary to the view generally accepted, *M. minor* is a far more serious pest than *M. piniperda.* The former attacks quite healthy pine trees for breeding purposes, and may continue to infest the crowns of the trees until the plantation is in a condition to be attacked by *M. piniperda.*

Little is known about the factors governing the distribution of *M. minor* in Britain. At present this species appears to be confined to Scotland and is most numerous in the eastern portion of the country. It seems probable that its introduction into Britain is of comparatively recent date, and it appears to have extended its range during recent years. With the extension of pine areas in the future, it seems probable that the range of *M. minor* will be greatly increased unless energetic measures are taken to prevent this taking place. The subject is of considerable importance and is therefore included within the scope of this investigation.

The effect of competition between different species of pine beetles is of particular interest in the case of *M. minor* and *Crypturgus cinereus,* Hbst. Much attention has been given to this subject in Russia during recent years. Stark (1926), in discussing the relation between the development of these two species, states that *C. cinereus* is not a primary pest of forest trees, as it hardly ever penetrates the bark of the trees, but normally utilises the galleries made by various other bark-beetles, chiefly *M. minor.* The entry of *C. cinereus* into the galleries of *M. minor* usually corresponds with the oviposition of the latter. Several pairs of *C. cinereus* may enter the same *M. minor* mother-gallery and form separate galleries on each side of the original gallery, destroying any eggs of the host that chance to be in the way. Thus, in the years of abundance of *C. cinereus* it is practically impossible to find normal galleries of *M. minor.* Under normal conditions *C. cinereus* may be regarded as a powerful natural controlling factor. On the other hand, in case of an outbreak of *M. minor,* owing to exceptional favourable conditions, as for example, forest fires, heavy wind-falls, etc., *C. cinereus* suffers most, as, in this case, the flight of *M. minor* is somewhat protracted and the bark-beetles overpopulate the trees, thus creating unfavourable conditions for itself as well as for *C. cinereus.*

Yakubyuk (1927), discussing the same subject, states that where *C. cinereus* was not present, *M. minor* developed normally, but where the former occurred no living individuals of *M. minor* were found, and that it has been definitely ascertained that *C. cinereus* attacks and kills the latter. The author states that he has seen several instances of *C. cinereus* eating the abdomen of living *M. piniperda* and *M. minor.* The same author (1928) published further notes confirming previous observations, that *C. cinereus* attacks other bark-beetles, particularly *M. minor.*

Prozorov (1929), writing on the same subject, states that the activity of *M. minor* is to a certain extent checked by *C. cinereus,* which destroys all stages in the galleries.

Crypturgus cinereus, Hbst., is not a British breeding species, so far as is known, but has been recorded as having been introduced into this country (Hallett, 1923) in mining timber.

The above observations indicate that the species might prove to be a useful addition to the fauna, but its introduction and establishment could only be considered after careful verifications of the above statements by extensive laboratory breeding experiments.

VI. Silvicultural Treatment and Forest Hygiene.

1. Treatment of young Pine Stands.

In all pine areas there is a resident population of insects, which, although potentially capable of becoming extremely injurious when conditions are favourable for their more or less unrestricted increase, may nevertheless be present in fairly large numbers without causing appreciable damage. The insects are only of economic importance when they actually cause a reduction in the value of the crop, or seriously threaten to do so. Control measures should, therefore, be directed towards keeping the insect population below the level at which such damage is done. On the other hand, expenditure on the destruction of insects is not justified if the cost equals or is in excess of the amount of the damage that would have been done. Further, the collection or destruction of insects merely with the object of reducing their numbers to the lowest possible minimum may, in effect, be useless expenditure and a waste of time and effort, and may even result in more harm than good, as will be shown later.

The obvious retort to the above statement is that it is impossible to assess the value of damage until it has been done, and that there is no means of estimating the probable extent of damage or predicting when or under what conditions it will be caused ; or when the insect population is at a level below that at which economic damage will be caused ; or whether the population is under control, or is on the increase.

In the present state of our knowledge of forest entomology all this is unfortunately quite true, and it is precisely this lack of information on these vital questions and the need for a solution to these problems that justifies any investigation.

In the past much useful work has been carried out on various phases of the bark-beetle problem and on that of other pine insects, but unfortunately there has been no definite systematic plan of campaign ; the work has been disjointed and sporadic, and no attempts have been made to correlate the detached and isolated observations and weave the whole into a complete and unified scheme of control. Control should aim at preventing damage, not merely at killing immense numbers of insects that ought never to have been allowed to breed. Unfortunately, the importance of insect control in pine areas is frequently ignored until an " outbreak " occurs, by which time the crop is often completely ruined, and the cost of destruction of the insect is an additional charge on what is already a financial wreck. The only really profitable investment in insect control is that which is instrumental in preventing damage.

Vague references have, from time to time, been made as to the beneficial effects of silvicultural treatment in connection with the control of insect pests, but no attempt has been made to indicate what exactly is meant. Frequent references are also found in " bark-beetle " literature to the desirability of " clean forestry." The attractiveness of this phrase probably lies in the popular conception that the reverse implies something dirty and unpleasant. The term may, within certain limits, be usefully employed, but the generally accepted idea that dead branches, or even logs or whole trees left lying in the forest, constitute a menace is without foundation. Once the bark has begun to decay or become loose, which usually takes place within a year of the death of the tree, there is not the slightest risk, so far as bark-beetles are concerned, of this material becoming other than beneficial from the biological and ecological standpoints. Unfortunately, the significance generally attached to the term " clean forestry " conveys the impression that it is desirable or even imperative that the forest floor should be kept clean, and that young plantations in the pole stage should be kept free from dead poles. The removal of this material is not only undesirable but may be actually detrimental. The really critical period is while the bark is in a suitable condition for breeding purposes ; once this stage has been passed the material is of no further importance for breeding purposes. The danger of leaving large quantities of suitable breeding material lying about in the forest is a real one and should not be confused with the question of the disposal of material unsuitable for breeding purposes. Felled timber, whether in the form of large thinnings, or the final crop, must always be a source of danger, and will at all times require careful attention, but this aspect of bark-beetle control is extremely simple and ought to be clearly understood by everyone concerned. Heavy thinnings and fellings can always be foreseen, and failure to deal with the situation is merely negligence on the part of the person or persons responsible for the supervision of the work. The danger arising from the neglect cannot be overestimated, and it is in this connection that the term " clean forestry " has a definite practical application. Nevertheless, it is a fallacy to suppose that the solution of the bark-beetle problem lies entirely in the proper disposal of felled timber, lop and top, and wind-blown trees. The real problem lies in the control of the bark-beetle population throughout the rotation of the crop. By far the greater part of the damage caused by these beetles and other insects in pine areas is done during the early stages of the growth of the crop. It is the considered opinion of the present writer that the reduction in value due to these defects in Scots pine crops in England is seldom less than 50 per cent., while in many cases the reduction in value is considerably greater. In fact, crooked, forked, or otherwise misshapen stems are of such frequent occurrence that their presence is generally regarded as quite the normal state of affairs. It is not suggested that all structural defects in the stems of Scots pine are caused by insect damage, but there is abundant evidence to show that the insects chiefly responsible are pine-beetles and pine-shoot moths. Structural defects of this type are of most importance when they occur below the maximum height required for the production of telegraph poles ; above that height they are of relatively little importance. In the absence of insect attack, and under normal conditions, Scots pine might reasonably be expected to attain this height during the first 50 years. We may, therefore, regard the first 50 years as being the critical period during which it is of the utmost importance that the insect population should be kept well under control.

Under silvicultural conditions the nearest approach to natural forest conditions is to be found in young crops in the pole stage before they have received their first thinning. In such areas predators and parasites are very numerous and, for a time, a state of biological control exists, its duration being largely influenced by the rate of growth of the crop. The trees tend to be more uniform in size in the case of moderately slow-growing crops than in very rapidly-growing crops ; competition for light is less severe in the former, and fewer trees become suppressed and suitable for the breeding purposes of pine-beetles at any given age than in the case of the latter. The rate of increase of the pine-beetle population is determined by the amount of suitable breeding material that is available ; if the supply of suitable breeding material is limited, overcrowding takes place, resulting in great mortality among the brood. Overcrowding also facilitates the activities of predators, owing to the brood systems of the host becoming linked up. The percentage of parasitism also tends to be higher where the density of the host population is greatest. If the supply of breeding material equals or exceeds the maximum requirements of the bark-beetles, the factor of overcrowding ceases to operate and biological control by means of parasites and predators also tends to break down, and a large increase in the bark-beetle population is the result. If these favourable conditions continue, an outbreak is inevitable. The maximum amount of suitable breeding material in the form of suppressed trees occurs when the crop reaches its maximum density. This is a stage later than the correct time for making the thinning on silvicultural grounds, since the thinning should have been made before the crop actually reaches that stage. The age at which the crop requires thinning depends on the rate of growth, original density, etc. ; the rate of growth is influenced by soil and subsoil conditions, exposure, aspect, and elevation. Various combinations of these factors may result in the same rate of growth in several crops widely separated geographically, or in very different rates of growth in different parts of the same crop in any particular locality. Consequently, no definite time for thinning can be prescribed and no set of rules as to density at any given age can be applied even to all parts of the same crop. Each crop and each part of the crop should be thinned according to its requirements. In practice, thinnings can be carried out only periodically, and it is an advantage to have uniformity of growth throughout the crop, which is most easily attained when conditions are not favourable for exceptionally rapid growth. The most rapidly growing portion of the crop determines the age at which thinnings must begin and the frequency with which they must be carried out. Similarly, the most rapidly growing portion produces the largest quantity of suitable breeding material for bark-beetles during a given period.

In contemplating the problem of bark-beetle control in young pine stands, the desirability of maintaining the equilibrium between the bark-beetle population and that of their natural enemies seemed to be of primary importance. The first step towards an understanding of the problem obviously lay in the collecting of statistical evidence, in order to determine what set of conditions favour the increase of bark-beetles. With this object in view, a series of experimental areas were laid out in the New Forest in the spring of 1933. For this purpose an unthinned plantation of 25 years was considered to be the most suitable, but as there was no plantation of this age available, plantations of about 20 years and 30 years were selected for the purpose. One of these was in Lodge Hill Inclosure, and the other in Buskett's Inclosure. The plantation in Lodge Hill Inclosure was 10·85 acres in extent and was planted in 1912–14. The area was evidently originally laid out as a silvicultural experimental area, and was planted 4 ft. by 4 ft. with three rows of Scots pine and one row of Corsican pine, the fourth plant in each row of Corsican pine being replaced by another species. In one part of the area beech was the tree used for this purpose ; in another part Douglas fir, and in another part larch. The original composition of the plantation was, therefore :—Scots pine, 75 per cent. ; Corsican pine, 18·75 per cent. ; other species, 6·25 per cent. In nearly every case, the beech, Douglas fir, and larch had either died or had become so badly suppressed by the Scots pine, as to be no longer of importance as an integral part of the crop. Similarly, over the greater part of the area, the Corsican pine had been almost completely ousted. For the purpose of the present experiment, the plantation may therefore be regarded as a pure Scots pine stand. Before thinning took place the average density in the actual sample plots was 1,830 stems per acre ; roughly two-thirds of the original number of trees planted. After thinning, the average density was 1,180 stems per acre, or 43 per cent. of the original number of trees planted.

The plantation in Buskett's Inclosure was 3·2 acres and was planted in 1902 with Scots pine, 4 ft. by 4 ft. Before thinning took place the average density was 1,300 stems per acre, rather less than 48 per cent. of the original number of trees. After thinning, the average density was 800 stems per acre, less than 32 per cent. of the original number of trees planted. In both cases the thinnings were marked and carried out by the forest staff and represented the normal treatment.

For the purpose of the experiment the plantations were marked off in strips one chain in width. Each year every fifth strip was thinned. In the first year, 1933, the first, sixth, eleventh, sixteenth, etc. ; in the second year, the second, seventh, twelfth, seventeenth, etc. ; in the third, the third, eighth, thirteenth, eighteenth, etc., were thinned. During the first season the whole of the thinnings were left lying as they fell, so as to give rise to the normal bark-beetle infestation for the maximum amount of material in each age class, it being anticipated that the density of the infestation would vary according to the quantity and quality of the material produced by the thinnings in each area ; the density of the infestation could then be assessed and a comparison made between the infestations in the thinned and unthinned portions, and also between that of each crop.

For the purpose of collecting data, a sample plot, one chain by one chain, was marked off with white paint in each of the thinned strips, and another sample plot of the same size in each of the unthinned areas, each of the latter sample plots being separated from the thinned strips by a strip of the unthinned portion.

In order to arrive at an estimate of the density of the infestation throughout the area, the pine shoots which fell as a result of the bark-beetle attack were collected in all the sample plots, both in the thinned and unthinned areas. This does not give the actual number of the bark-beetles, but it does give a fairly accurate estimate of the density of the infestation in terms of damage done by the beetles which have emerged from the breeding material, it being an observed fact that, although *Myelophilus* will travel considerable distances in order to concentrate on suitable breeding material, they do not, on emerging as adults, immediately disperse throughout the forest in search of suitable food material, but attack the shoots at the apex of the crown of the trees in their immediate vicinity. A few beetles did attack trees just outside the thinned strips, but the majority attacked trees within the strips in which they were bred. This is clearly shown in the number and position of the fallen pine shoots.

Both species of *Myelophilus* bore holes into the shoots of pines and form feeding tunnels in the pith. One beetle may make several of these tunnels in one or more shoots, or several beetles may form separate tunnels in the same shoot. A strong shoot may contain several tunnels, but one tunnel is generally sufficient to cause the loss of the shoot. The attacked shoots fall off and may be seen on the ground in most pine woods in summer and autumn and throughout the winter. Plate VIII, fig. 3, shows the effect of a strong *Myelophilus* infestation. In this particular case the photograph shows part of a wood where the average density of the fallen shoots was, at that moment, 128,520 per acre. This figure does not represent the total number of shoots destroyed ; other shoots subsequently fell, bringing the total number of shoots destroyed to 168,900 per acre, as a result of the autumn attack. The beetles causing the damage spend the winter feeding in the bast of the bark at the base of the trees, and in the spring another attack on the crowns of the trees takes place, resulting in further loss of shoots. The above infestation was the result of a fire in an adjacent pine stand. In the majority of cases, the current year's growth is attacked and single shoots fall, but in some cases the beetles burrow into the previous year's growth and the twig breaks off just below the whorl of side branches, resulting in the loss of the whole of the current year's growth in the form of a multiple shoot. The ratio between the number of single shoots and multiple shoots which may occur has been determined during the course of the investigation by the examination of large numbers of shoots in infestations of various degrees of density. The list below gives particulars of some of these infestations.

Of the whole of the pine shoots collected from the infestations, 88 per cent. were single shoots and 12 per cent. were multiple shoots. It will be seen, therefore, that the maximum range in departure from the average ratio was only 5 per cent. in either direction, and is seldom more than 2 per cent., and that the ratio between the number of single and multiple shoots is not necessarily influenced by the density of the infestation, and is not directly proportional to the density of the infestation. The above figures include only Scots pine shoots. Although the method of assessment of the density of an infestation by means of the collection of pine shoots does not give the actual number of beetles concerned, the method is useful and provides a fairly accurate scale by which the intensity of an infestation may be measured in terms of damage resulting from the infestation. As the investigation proceeds, it may be possible to correlate the actual number of beetles in any given infestation with the number of shoots destroyed, and thus determine the density of the *Myelophilus* population in any given Scots pine stand. It will then be possible to use this method as a population indicator and enable the forester to regulate the beetle population and prevent damage which, though unobtrusive, is nevertheless of great economic importance. Further reference will be made to this subject when dealing with the question of billets and trap-stems.

The method adopted in the collection of shoots in the experimental plots was as follows : Two rows of trees were taken at a time, running in the direction of the long axis of the strip, and a line was run out to mark the boundary. The shoots lying between these rows of trees were collected, counted and booked. As the rows of trees were 4 ft. apart, this gave 8 sets of figures for each sample plot. In order to find out the rate of fall-off in the number of shoots on each side of the thinned strips, the shoots were collected in 4 double rows in the unthinned portion of the plantation bordering each side of the sample plot. Three collections were made during the autumn and winter, the last collection being made in March just before the shoots began to fall as a result of spring feeding. The figures were plotted to show a curve representing a section one chain wide running across the thinned strip and including half a chain of the unthinned area on each side (fig. 2).

No. of fallen pine shoots per acre	Percentage of single shoots	Percentage of multiple shoots
168,900	89	11
133,110	89	11
98,840	91	9
84,780	86	14
75,020	84	16
74,700	85	15
46,480	87	13
21,120	88	12
18,660	87	13
7,910	89	11
7,840	84	16
6,480	89	11
3,590	90	10
2,190	86	14
2,140	83	17

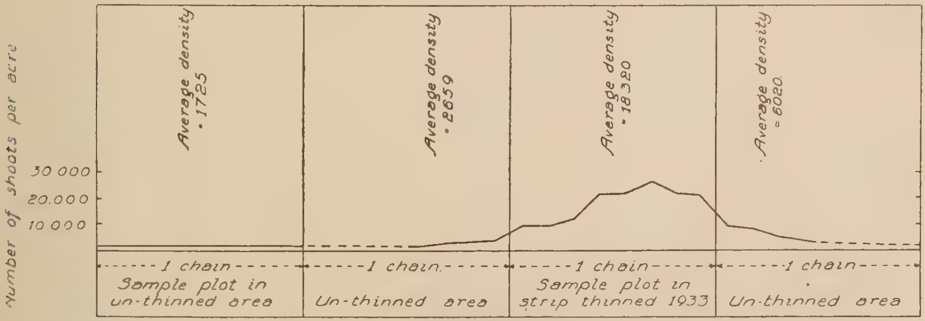

Fig. 2.

The above curve shows the average density of the infestation in the sample plots in Lodge Hill Plantation during 1933, and the following curve shows that of Buskett's Inclosure for the same year (fig. 3).

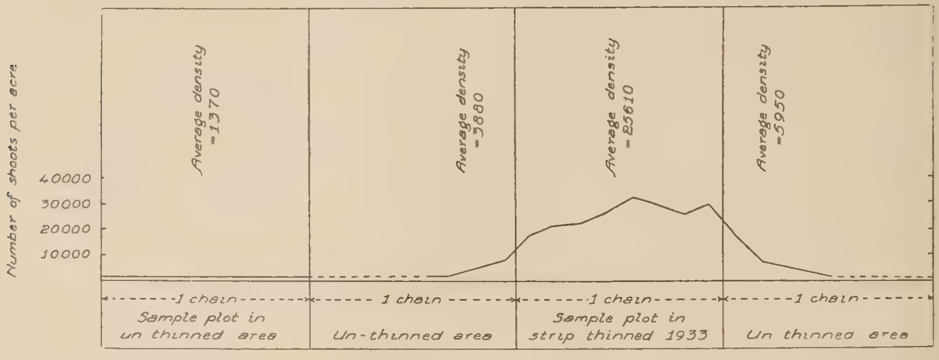

Fig. 3.

It will be seen that the maximum density of the infestation lies within the limits of the thinned strip and diminishes on each side until at a distance of half a chain from the source of the infestation the level is almost identical with that of the sample plot in the unthinned area. The felled poles in all the sample plots were measured in order to ascertain for each experimental area—the total area of bark per acre ; the number of shoots per 100 sq. ft. of bark ; the area of bark on material over 3 in. diameter and under 3 in. diameter ; the volume of material per acre over 3 in. diameter ; the percentage of rough bark and smooth bark on material under 3 in. diameter. The results are tabulated below (Table IX).

It will be seen that there is little difference between the total superficial area in each case, but there is a considerable difference in the number of pine shoots per 100 sq. ft. of bark. The percentage of bark on material over 3 in. diameter in Buskett's is double that in Lodge Hill.

The whole of the poles in one of the sample plots in Buskett's were then measured to find the total area of rough bark as compared with smooth bark, the figures were : rough bark 31 per cent., smooth bark 69 per cent. ; almost identical with those for the material under 3 in. diameter in Lodge Hill, but showing a big contrast with the figures for the material under 3 in. diameter in Buskett's.

The whole of the bark was then removed from the poles and the *Myelophilus* egg-galleries counted and measured. The results showed that 73 per cent. of the galleries were in the rough bark as compared with 27 per cent. in the smooth bark. The rough bark contained 246 galleries and the smooth bark 41 galleries per 100 sq. ft. Earlier in the season a quantity of material examined in Knightswood gave the following figures :—Rough bark 511 sq. ft., 1,901 galleries—372 per 100 sq. ft. ; smooth bark 826 sq. ft., 515 galleries—62 per 100 sq. ft. It will be seen that the ratio was 6 : 1, exactly the same as in the case of Buskett's, although the density of the infestation was 50 per cent. stronger in the Knightswood material.

The average of 246 galleries per 100 sq. ft. in the most suitable breeding material in the Buskett's experiment showed that overcrowding had played very little part in restricting the bark-beetle increase in this case. The average length of the egg-galleries was 4¼ ins. The total number of *Myelophilus* galleries in the sample plot of one-tenth of an acre was 648—6,480 per acre. Allowing an average of 120 beetles per gallery, the potential population would be 777,600 per acre. The total number of shoots destroyed as a result of the actual infestation was only 30,525

TABLE IX.

Experimental areas 1933	Area of bark per acre	Total number of pine shoots	Number of shoots per 100 sq. ft. of bark	Area of bark on material over 3 in. diam.	Per-centage	Area of bark on material under 3 in. diam.	Per-centage	Volume of material over 3 in. diam.	Percentage of rough bark on material under 3 in. diam.	Percentage of smooth bark on material under 3 in. diam.
Lodge Hill ...	5,338 sq. ft.	22,660	425	1,072 sq. ft.	20	4,266 sq. ft.	80	64 cu. ft.	31·6	68·4
Buskett's ...	5,873 sq. ft.	30,525	520	2,380 sq. ft.	40·5	3,493 sq. ft.	59·5	133 cu. ft.	9·7	90·3

per acre, 4·71 per *Myelophilus* gallery, or an average of 5·2 per sq. ft. of bark on the available breeding material, taking the amount of bark in the average of the sample plots, which is rather lower than the figure for the particular sample plot in question. These figures suggest very heavy mortality among the *Myelophilus* broods. In examining the bark on the poles in the above sample plot, the parasite larvae were found in the *Myelophilus* pupal chambers in the bark and between the bark and the timber. The number found in the thin-barked material was 2,835, or 1,629 per 100 *Myelophilus* galleries. Where the bark was thick, no parasite larvae were found between the bark and the timber, and the bark had to be broken in order to find them. This method produced only 284 parasite larvae per 100 *Myelophilus* galleries. In order to find a factor which would represent a more accurate estimate of the population, a quantity of thick bark was placed in breeding cages at Farnham House Laboratory and the parasites allowed to emerge as adults. This material produced 765 parasites per 100 *Myelophilus* galleries. On this basis, the parasite population in Buskett's would be :—

Rough, thick bark	765 per 100 galleries	...	36,260 per acre.
Smooth, thin bark	1,629 ,, ,, ,,	...	28,350 ,, ,,
	Total per acre ...	...	64,610

This means eleven parasite larvae per square foot of bark ; more than double the number of shoots destroyed as a result of the infestation. The above figures refer only to the generation of parasites which overwintered in the larval stage. One generation of parasites had completed its cycle and emerged from the thin bark during the summer, as was shown by the numerous exit-holes, but no parasite exit-holes were found in the thick bark. The reason for this doubtless was the fact that the *Myelophilus* larvae were inaccessible to the parasites until they burrowed into the bark to pupate late in the summer. In many cases the whole of the *Myelophilus* larvae in the thin bark had been destroyed. In the whole of the material there was evidence of heavy mortality among the bark-beetle broods, due to predators. The writer is of the opinion that predators are of greater importance than the parasites as controlling factors in the case of bark-beetles, especially in the thick-barked material.

The parasite larvae are not collected until February, and it is probable that a large proportion of the parasite population had by then been destroyed by the numerous Dipterous larvae and by *Thanasimus* larvae, many of which were found in the bark-beetle brood-galleries. The evidence of the above data suggested two courses by which the bark-beetle population might be reduced to a very low level during the following season, either by the elimination of all material over 3 ins. in diameter, or by the elimination of all the rough-barked material. The latter course was adopted in 1934, when the thinning was made in that year. A 6 ft. length was cut off the butt end of each pole ; all these 6 ft. butt lengths were buried in a slanting position with the thin end slightly projecting above the surface to act as breeding material for *Hylastes ater* and *Hylobius abietis*, in order to utilise the material for the study of the effects of predators on the development of these species and at the same time render the material inaccessible to *Myelophilus*. The result of this operation is reflected in the returns for the collection of fallen pine shoots during the winter of 1934 (fig. 4).

In the case of the Lodge Hill experiment the total number of shoots produced by the infestation resulting from the breeding material was actually less than the average per acre in the unthinned portion of the area.

In the case of the Buskett's experiment (fig. 5), the infestation was slightly higher, but even within the actual thinning, where the maximum density occurred, the density was less than one shoot per square yard. The difference in density between the two infestations in 1934 is probably accounted for by the fact that the thinning in Lodge Hill was rather lighter and the material smaller. In Lodge Hill there were only 2,756 sq. ft. of bark per acre, as compared with 3,475 sq. ft. per acre in Buskett's. In the latter case the total area of bark corresponded almost exactly with the area of bark on the material under 3 in. diameter in the 1933 experiment.

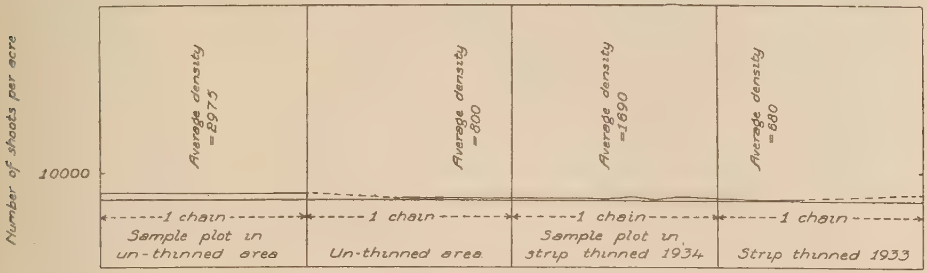

Fig. 4.

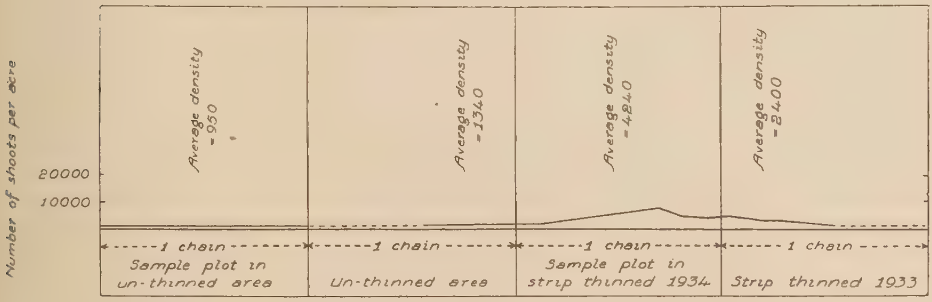

Fig. 5.

The results of the 1934 experiment clearly demonstrate that there is no risk of a *Myelophilus* outbreak as a result of leaving small diameter, thin-barked material on the ground, when thinnings are made in Scots pine plantations. The next step was to produce evidence to show that the reduction in the density of the bark-beetle population was not merely due to a seasonal fluctuation. The obvious way to do this was to reverse the process, and by providing an excess of suitable breeding material in both experimental areas, cause an abnormal increase in the bark-beetle population. In order to do this it would be necessary not only to provide sufficient breeding material to prevent the operation of the factor of overcrowding among the brood, but also to eliminate as far as possible the parasites and predators. Overcrowding could most easily be avoided by providing large-diameter material. Parasites would be rendered least effective by using thick-barked material, and predators would be most effectively excluded by raising the most suitable breeding material off the ground, since they tend to be most numerous in material which is in contact with the ground.

It seemed desirable that the sudden increase should occur simultaneously in both areas. It was therefore decided that both areas should be treated alike, as in the previous years. In view of the above facts, the method of treatment decided on was to cut off a 6 ft. length from the butt of each of the poles ; this would include practically the whole of the thick bark. The 6 ft. butts from one strip were then transferred to another strip, so as to provide double the quantity of thick-barked material in the latter strip and none in the former. The smooth or thin-barked portions of the poles were placed about 4 ft. apart on the ground and the 6 ft. butts were laid across and upon these poles in order to keep the thick-barked material off the ground and thus reduce the risk of attack by predators to a minimum. In this way, all the requirements for the production of an abnormal infestation were provided. Sample plots were then marked out as in the previous years.

The subsequent collections showed that the desired object had been achieved. The average density within the augmented strip in Lodge Hill was 76,520 shoots per acre (fig. 6).

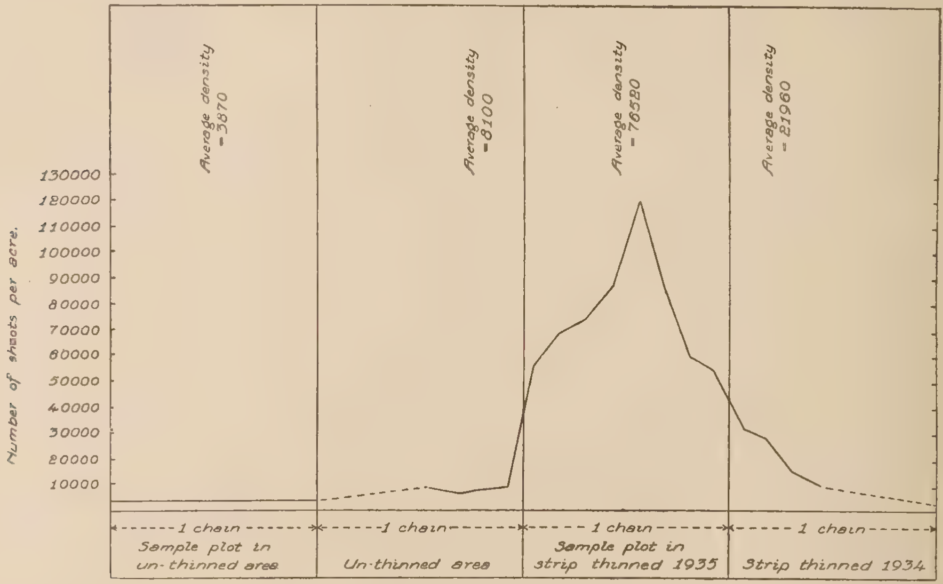

Fig. 6.

While the average density in the augmented strip in Buskett's was 75,020 shoots per acre (fig. 7).

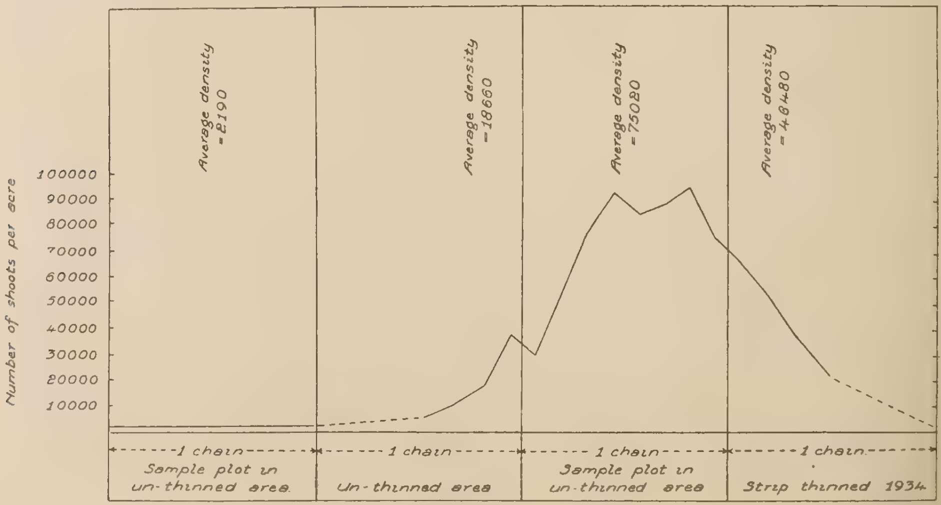

Fig. 7.

The total number of shoots collected within the sample plots and in the half-chain belts bordering each side of the sample plots showed that the actual infestation produced was greater in Buskett's than in Lodge Hill. In the former the total number of shoots was 107,590 per acre of breeding material and in the latter 91,550. The lower average density within the sample plot in the thinned area in the Buskett's experiment was due to the greater degree of dispersal of the bark-beetle population in this case. It will be seen that in both cases dispersal into the previously thinned area was greater than into the unthinned area. The more abrupt fall-off in the unthinned portion of Lodge Hill than in the case of Buskett's was doubtless due to the difference in density of the two crops. The density of the unthinned area in Lodge Hill being 1,830 stems per acre, while that of the unthinned area in Buskett's was only 1,300 stems per acre. The latter crop is, of course, 10 years older than the former. Notwithstanding the lower degree of dispersal into the unthinned area in the case of Lodge Hill, it will be observed that there has been a gradual rise in the average density of the bark-beetle population as indicated by the fallen pine shoots in the area during the past three years, the figures being :—

1933 ... 1,725 fallen shoots per acre
1934 ... 2,975 ,, ,, ,, ,,
1935 ... 3,870 ,, ,, ,, ,,

It will be seen that the average density in the unthinned area bears no relation to the density of the infestation in the experimental plots during the corresponding years.

In the case of Buskett's there has been no gradual increase in the density of the bark-beetle population in the unthinned area, although there has been a slight fluctuation, the maximum number of shoots per acre being 2,190 in 1935, which is actually lower than the number in the unthinned area in Lodge Hill in 1934, when the infestation in the experimental area was at its lowest. The difference in the average density of the bark-beetle population in the unthinned portions of the two areas can only be attributed to the greater degree of efficiency of the resident parasite and predator population in the longer established crop.

The particulars of the experimental plots for 1935 are as follows :—

Experimental areas 1935	Total no. of fallen shoots per acre	Total area of bark per acre sq. ft.	Area of smooth bark sq. ft.	Area of rough bark sq. ft.	Percentage of rough bark on material over 3 in. diameter	Percentages of rough bark on material under 3 in. diameter
Lodge Hill	91,550	7,699	4,603	3,096	30	70
Buskett's Lawn	107,590	9,937	5,469	4,468	53	47

It is evident that the quantity of material available was greater than the requirements of the bark-beetle population, as the difference in the quantity of rough bark was sufficient to cause a much greater difference in the density of the resulting infestations if the material had been fully utilised. The resident population of bark-beetles was, of course, extremely low in both experimental areas at the beginning of 1935, as shown by the figures for the 1934 infestation.

That the strong infestations produced in 1935 were directly due to the presence of an abundance of suitable breeding material and to the exceptionally favourable breeding facilities provided, and were not the result of seasonal fluctuation, is clearly shown by the figures for the sample plot in the thinned strip in the Buskett's area, from which the 6 ft. butt lengths had been removed (fig. 8).

In this case the average density of the fallen shoots in the sample plot within the thinned strip was only 7,910 per acre, and the total infestation produced was only 12,220 shoots per acre of breeding material. The quantity of material in this case was 4,266 sq. ft. of bark per acre, as compared with 3,475 sq. ft. per acre in the same experimental area in 1934. The additional 791 sq. ft. of bark per acre in 1935 resulted in an infestation which produced exactly twice the number of fallen pine shoots. An infestation of this intensity is not serious, as it represents less than 3 pine shoots per square yard during the whole of the period August to March, but it must be remembered that in this case all the rough or thick-barked material had been eliminated; a smaller quantity of material which included the normal proportion of rough bark would probably result in a much stronger infestation.

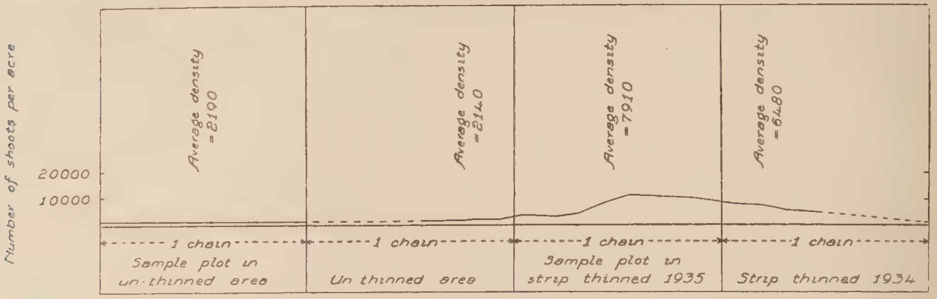

Fig. 8.

It is regrettable that lack of funds prevented a census of the parasite population during the winters of 1934 and 1935, in which case the data would have been more complete and of greater value.

No thinnings have been made in the Lodge Hill and Buskett's experimental areas during the spring of 1936, the intention being to carry out thinnings in July, so as to note the effect of thinning after the main breeding season of *Myelophilus* is over, and also to ascertain whether the thinnings cut at this date remain in a suitable condition and are attractive for breeding purposes during the following spring. The progress of the increase in the bark-beetle population will also be noted in the unthinned areas.

The foregoing experiments have produced some very useful results, but in the opinion of the writer they were not on a sufficiently large scale to meet the requirements of the case. It must be remembered that the thinnings were carried out in strips one chain in width at intervals of five chains in order to facilitate the working of the experiments and to accommodate the experiments to the size of the areas available. It therefore seems desirable that the experiments should be repeated on a large scale with modifications so as to compare the effects of thinning in strips of various widths, with the results obtained by the normal practice of thinning simultaneously throughout the stand.

The results of the experiments indicate that it would in all cases be a distinct advantage if the first thinning in Scots pine stands could be deferred until the crop had reached the size at which the removal of all saleable produce would include all the rough-barked material. The data show that at 20 years of age the material under 3 in. diameter in Lodge Hill included 31·62 per cent. of rough bark, while at 30 years of age in Buskett's, the percentage of rough bark on material under 3 in. diameter was only 9·68 per cent. Regarded from an entomological point of view, the results of the investigation indicate that it is desirable to defer the first thinning of Scots pine stands until the time approaches when the combined effects of overcrowding and biological control threaten to break down. This point is reached when the quantity of suitable breeding material in the form of suppressed trees tends to equal the minimum requirements of an increasing resident bark-beetle population. The age at which this stage is reached may vary not only for crops in different localities, but also for different parts of the same crop, as the rate of growth will always be influenced by such factors as aspect, altitude, exposure, soil, subsoil, etc. The original planting distance is also a factor of importance. A superficial consideration of the above statements may suggest that these objectives would most easily be attained by wide spacing of the plants on soils and situations suitable for exceptionally rapid growth, but in practice this does not prove to be the case. A dense crop of natural regeneration on comparatively poor, sandy soil can be maintained at a greater density and for a longer period without risk of a pine beetle outbreak, and may ultimately produce a more valuable and more profitable yield.

The primary object of carrying out the thinnings in strips and leaving the small diameter, thin-barked material on the ground is to provide a sustained but limited supply of breeding material for the maintenance of a permanent population of parasites and predators. This population subsists largely on hosts which are of secondary economic importance, such as *Hylurgops palliatus*, and also *Pissodes notatus* and *Hylastes ater*. The latter species normally breeds in the roots below ground-level, but is induced to breed on the surface in the material thus provided. There is also a saving in expenditure which would otherwise be incurred in the removal or destruction of the material. More important, however, is the beneficial effect of the disintegration of the material and the formation of a richer humus which will improve the quality of the forest soil.

2. The Use of Billets and Trap-stems.

Although the use of billets and trap-stems for the control of pine beetles has frequently been advanced in a general sort of way, little precise information exists as to the results which have been obtained or may be expected from their use. It is generally assumed that the use of trap-stems is a perfectly simple matter consisting merely of the preparation of stems by means of the removal of a ring of bark in order to bring the selected tree into a sickly condition, and the subsequent removal and destruction of the bark before the pine beetles complete their development. In practice, however, the procedure is not so simple and straightforward, and there is no certainty that the indiscriminate preparation of stems or billets and the removal and destruction of the bark will have the desired effect in many cases. On the contrary, it may ultimately result in a chaotic series of interactions by combinations of factors cancelling out the effects of each other and end in futile effort and much useless expenditure.

Sedlaczek (1921) has shown that a wide range of conditions may be produced by various modifications of the method of preparing stems, by differences in the season of the year when the stems are prepared, the position of the stems in relation to their surroundings, and whether the stems are constantly shaded or occupy sunny situations. The present writer has found some of these points to be of great importance, particularly with regard to the attractiveness of the stems to parasites and predators. It is in this connection that trap-stems are of particular interest and utility. They may prove to be of the utmost value in eliminating certain types of predators which may be undesirable and to which reference has already been made. The utilisation of billets and trap-stems to facilitate the effects of over-crowding and desiccation is also a subject of the utmost importance. It will be seen from the above remarks that the use of billets and trap-stems in connection with bark-beetle control covers a wide range of possibilities, both positive and negative. An exhaustive study of these possibilities will be made on a large scale under various forest conditions. This stage of the investigation could not be undertaken until a fairly comprehensive knowledge of the parasites and predators and of all the relevant factors had been acquired. A detailed study of the use of billets and trap-stems necessitates a preliminary assessment of the local factors which determine the rate of growth and density of the crop, a description of the crop, an approximate estimate of the density of the bark-beetle population, a description of each type of tree selected, whether suppressed or dominant, etc., rate of growth and condition when selected for use, particulars of size, method of preparing, date when prepared, and a description of the environmental factors. The examination of sample stems of each series is necessary from time to time, in order to note the density of attack and the progress of development of the broods, the effects of overcrowding, the presence and time of appearance of the various parasites and predators, and their effect on the bark-beetle population. The interaction of the various predators, the number of bark-beetles that complete their development, and the effects of the various predators on the overwintering parasite larvae, with special reference to *Thanasimus formicarius* and Diptera, must also be considered.

It is anticipated that in this way useful information will be collected as to the best type and size of tree to use and method of treatment for the following purposes :—

(*a*) The direct control of the beetles.

(*b*) The destruction of the bark-beetle broods by facilitating overcrowding.

(*c*) The premature destruction of the broods by causing desiccation.

(*d*) The encouragement of the most desirable species of parasites and predators by providing the particular combination of environmental factors most attractive and necessary for their successful development.

(*e*) The provision of conditions most attractive to the undesirable species of predators with the object of their destruction.

Observations have already been made which indicate that a simple scheme might be evolved by means of which the use of billets and trap-stems can be made practicable and effective. The period of their greatest usefulness is probably during the late pole-stage of the crop and on to the end of the rotation.

3. Forestry Operations which tend to upset the Balance.

It not infrequently happens that individual trees or small groups of trees are blown down in more or less remote areas, or at times when pressure of work causes their presence to be ignored until after they have been used by bark-beetles for breeding purposes. At a later date these trees may be removed for use as timber or firewood. An examination of large numbers of trees lying in the forest in various parts of the country has shown that the removal of these trees during the autumn or winter may result in the loss of large numbers of predators. For example, 50 sq. ft. of bark on a single Scots pine log examined in October 1933, on the Seafield estate in Scotland, yielded the following species :—664 *Rhizophagus ferrugineus* adults, 7 *R. dispar* adults, 2 *R. depressus* adults, 11 *Pityophagus ferrugineus* adults, 8 *Glischrochilus quadripustulatus* adults, 144 *Pityophagus ferrugineus* larvae, 6 *Thanasimus formicarius* larvae, and several *Rhizophagus* larvae.

This cannot be regarded as representing the total predator population of the log, as no doubt a large number of *Rhizophagus* adults were concealed in the crevices of the thick bark. The figures must not be taken as an indication of the relative numerical abundance of the various species in Scotland. In 1932 a number of logs were examined on the Atholl estate in Perthshire and on that occasion *Rhizophagus dispar* was found to be the most numerous species. This was also found to be the case in Lancashire in 1933.

The presence of these predators under the bark in winter is not confined to Scots pine ; a large larch log, examined in Verulam Woods, Herts, in 1932, yielded

615 *Rhizophagus* adults, while Weymouth pine and spruce in the same woods were found to be heavily populated.

The examination of a dozen small Scots pine logs in the New Forest, with an average of about 40 sq. ft. of bark, yielded an average of over 300 *Rhizophagus ferrugineus* adults each during September 1934.

The bark of standing dead trees in winter often contains large numbers of predators. *Rhizophagus bipustulatus* appears to prefer dead standing trees for hibernation purposes, and was found clustered in hundreds under the bark of dead Scots pine at Woburn, and under the bark of dead spruce at Verulam. It will readily be seen that the removal of these logs in winter will have a serious effect in depleting the predator population. This can, however, be avoided by removing the bark and allowing it to remain in the forest when the timber is removed. The bark at this stage is not firmly attached to the logs and may easily be pulled off.

If logs have been lying only one summer in the forest and are removed during the following autumn or winter, the bark may contain large numbers of parasite larvae in addition to predators. Reference has already been made to the fact that the removal of Scots pine thinnings during the autumn or winter may result in the loss of more than 64,000 parasite larvae per acre.

4. Control Measures in Felling, Burnt, and Windfall Areas.

In cases where exceptional facilities for abnormal increase in the bark-beetle population occur, control measures must, at present, be of the most simple description, in order that they may be put into operation and carried out with the minimum risk of misunderstanding or mismanagement.

(*a*) *Felling Areas.*

The control of bark-beetles in felling areas is the least complex aspect of the problem of bark-beetle control. The extent of the operations, and consequently the amount of risk involved, is known in advance and the necessary steps can be taken with the situation.

Although felling areas provide exceptional facilities for the rapid increase of bark-beetles, if the operations are carried out without regard for the elementary rules of forest protection, there is no reason why the beetles should be allowed to increase in felled timber. Any increase that takes place in their numbers, due to felling operations, should be regarded as the result of negligence on the part of the persons in charge of the forest.

The treatment of felled areas may have for its objective either the prevention of increase or the actual reduction of the bark-beetle population. If the object in view is merely the prevention of increase, this may be brought about either by rendering the bark unsuitable for breeding purposes by the application of chemicals, or by the complete removal of the bark. An experiment designed to test the relative efficiency and comparative cost of these two methods was carried out in the New Forest during 1935. Six sets of logs were included in the experiment, three sets were treated with different chemical sprays, the fourth set was completely barked, the fifth set barked in strips, and the sixth set was used as controls.

There was considerable difference in the results obtained by the chemical treatment, but in no case was it found satisfactory or efficient, and the actual cost of the operation in labour alone was in excess of the cost of completely barking the timber. The additional cost of preparing and transporting even the cheapest and simplest form of spraying material at once renders the method prohibitive. The difference in the cost of strip barking as compared with the complete removal of the bark is negligible, but strip barking did not give entirely satisfactory results. The above experiment was carried out on a rather small scale, and it was possible to have the logs lying in the open free from lop and top, thus providing maximum facilities for the application of the spray. Under normal felling conditions the difficulties of efficient application of the spray would be greatly increased, and it seems probable that the degree of efficiency would be correspondingly lower. Treatment of the logs with chemicals with a view to preventing the beetles breeding in the bark has the great disadvantage that the work must be completed before the flight period begins, which may be as early as the middle of February. Any trees felled after the flight period has commenced would have to be treated immediately, as the lapse of a few hours might render the operation futile. Another great disadvantage of treatment with a view to preventing the beetles breeding in the material is the fact that the results are entirely negative ; it merely deprives the insect of the facilities for breeding in the certain specified material, but does not prevent them from breeding in the suppressed trees in the surrounding stands. Barking the timber for the purpose of preventing the beetles breeding in the material has only the same effect as spraying with chemicals, except that barking gives 100 per cent. efficiency. These results are good so far as they go, but it would be a mistake to regard them as satisfactory from the viewpoint of insect control. They are merely defensive. To be really effective, control measures must have as their objective the maintenance of the bark-beetle populations at a level at which the risk of damage to the crop is reduced to a minimum. Felling areas not only provide exceptional facilities for bark-beetle development, they also provide unique opportunities for the reduction of the general level of the population, and every effort should be made to utilise these opportunities to bring about the desired results. The sudden increase of suitable breeding material causes a concentration of bark-beetles from the surrounding pine stands ; the beetles should be allowed to attack the bark of the felled timber for breeding purposes and the bark should be left attached to the logs until the whole of the eggs have been laid and the larvae have become well-developed. This will normally have taken place by the end of April in the South of England. By this time a large proportion of the timber will probably have been converted. The remainder of the timber should now be barked as rapidly as possible so as to complete the operation before the larvae burrow into the bark to pupate. In the case of *Myelophilus minor* the larvae often burrow into the sapwood in thin-barked material. In the North of England and in Scotland, the date when barking should commence will be later. The dates will also vary considerably according to whether the season is early or not. An examination of the material is necessary in each case to ascertain the state of development of the brood. In all cases the first brood is of the utmost importance, as parasites and predators are least effective in the case of early breeding beetles. The evidence collected to date indicates that the second brood is of little importance on account of the activities of the parasites and predators. Considerable attention is being paid to this aspect of bark-beetle control, particularly in standing woods, and much work remains to be carried out.

The time required to bark a given quantity of material will vary according to the nature of the material, the lie of the land (whether flat or very sloping), and other factors, but an accurate estimate can be made in each case by carrying out a small-scale experiment. It will then be possible to estimate the number of men required to carry out the work in the specified time. The necessity for carrying out the work at the proper time cannot be too sharply emphasized, as success or failure depends on this, and the performance of the work at the wrong time will result in useless expenditure. The bark need only be roughly removed. The complete removal of all the bast is not necessary, as in the case of peeling telegraph poles, and there is no comparison between the cost of the operations.

During the process of barking, a large proportion of the parent bark-beetles are killed, and as the ones which escape are spent they are of little importance. The bark should, therefore, be allowed to lie in the forest where it falls and should not be collected and burned, as this operation not only delays the really useful work, but also entails much useless expenditure, since most of the bark-beetles that have not been killed will have crawled away or taken flight before the bark is burned. On the other hand, large numbers of *Rhizophagus* adults are invariably present. The latter do not readily take flight, but conceal themselves among the crevices of the bark and are therefore more likely to be destroyed if the bark is burned. If the barking is carried out expeditiously, the work should be completed before many of the parasites have oviposited ; destruction of predators and parasite larvae will therefore be reduced to a minimum, while destruction of the bark-beetle brood will be at its maximum. Barking the timber before the pine beetles have completed their egg-laying is futile, as the insects fly off to find other breeding material.

The disposal of lop and top in felling areas is in practice largely a matter of expediency. There is not much risk of *Myelophilus* increase in this material, except perhaps in the largest limbs and rough tops. If it can be destroyed before the beetles emerge, so much the better, but after the end of July the lop and top contains few injurious insects and if burned between August and the following May, parasites and predators will be destroyed in considerable numbers. This, however, cannot always be avoided, and provided that the barking of the timber has been efficiently carried out, any parasites and predators present in the lop and top can legitimately be sacrificed to facilitate the routine work and thus compensate to some extent for the trouble taken over the more important control measure. When, however, the lop and top is dealt with, it should be burned on the stumps of the late crop in order to render them more attractive to Cerambycids ; the larvae of the latter feed in the bark, thus contributing towards the control of the pine weevil, *Hylobius*, by using up and destroying its food supply. It has been stated above that the number of fallen pine shoots occurring as a result of an infestation may perhaps be correlated with the actual number of the pine-beetle population ; in which case the problem of beetle control will be considerably simplified. For example, if it can be shown that the resident *Myelophilus* population in a given Scots pine stand is, say, 10,000 per acre in the autumn of any particular year, it may safely be assumed that, in the absence of other sources of infestation by invasion, the population in the following spring will be less than 5,000 pairs of potential parent beetles per acre. It will then be possible to calculate the amount of breeding material which will be required to attract and accommodate that number of insects and the necessary material can then be provided in the form of rough-barked billets of the type found to be the most attractive. Testing and demonstrating this method will naturally be rather a lengthy process. In the meantime, barking the timber appears to be the only safe procedure.

(*b*) *Burnt Areas.*

The chief difference in dealing with the control of bark-beetles in burnt areas, as compared with felling areas, is that whereas in the latter case the occurrence and extent of the areas to be dealt with can be foreseen and provision made in advance for dealing with the situation, in the case of burnt areas the situation arises spontaneously and may involve a wide range of different classes of material, necessitating entirely different treatment. In one respect the two cases are similar ; the control measures must be of the most simple description. No time must be lost in dealing with the situation. If the burnt trees are large enough for timber, the area should be treated as a felling area and in the same way. If the material is only fit for pitwood, the best plan is to clear the area immediately before the bark-beetles have time to breed. Market considerations should be subordinate to the requirements of efficient control measures.

If the trees are too small for pitwood or fencing material, by far the best and safest plan is to pull all the trees out by the roots, by means of a small tractor if necessary, and burn the whole of the material on the spot. This will be by far the cheapest and most efficient method of treatment, as it prevents both bark-beetles and pine weevils from increasing greatly, as is likely to be the case if drastic treatment is neglected. It must be remembered that there will be something like 2,000 roots per acre for weevils to breed in if the trees are merely cut off, and an average of only 10 weevils per root would produce a large population, which might cause serious damage and considerable expense. If the situation is dealt with energetically, risk of insect damage is entirely eliminated ; the area can be replanted immediately, and the loss reduced to a minimum. Failure to deal with the situation immediately may have disastrous results, of which examples could be cited.

(*c*) *Wind-blown Areas.*

As in case of burnt areas, the only safe way is to treat the situation as a state of emergency, cut the loss and eliminate all danger of insect damage to the uninjured crops. Dilatory and feeble attempts to salvage is false economy, and invariably end in additional loss. In the case of either extensive windfalls or fire, a rapid survey will soon reveal the extent of the affected area, and if the stock maps and description of compartments have been kept accurately up to date, a few simple calculations will provide an estimate of the nature and quantity of material to be dealt with. The number of men and the description and quantity of plant and equipment necessary to deal with the situation within a specified time can easily be accurately estimated. Trägårdh and Butovitsch (1935) have shown that delay in dealing with wind-blown timber may result in the damage being multiplied indefinitely.

VII. Summary and Conclusions.

1. The object of the investigation is the study of possible methods of control of injurious insects in pine areas in Britain, with special reference to bark-beetles and to *Myelophilus piniperda*, L., in particular.

2. Reference is made to the economic status of the pine beetles in Britain as compared with other countries, and it is pointed out that in this country control measures must be of a more intensive character than in countries where large tracts of natural forest occur.

3. An analysis of the various types of damage caused by *Myelophilus* is made, and it is shown that although the actual amount of damage caused in any particular year may at the time appear comparatively slight, the effects of successive outbreaks are cumulative, and frequently result in a great reduction in the value of the crop.

4. The occurrence of bark-beetle outbreaks and the conditions under which they occur are briefly described.

5. The factors influencing the pine beetle population are discussed, and it is pointed out that the effects of climatic and physical conditions on the development of the host-plant under forest conditions are of fundamental importance in determining the density of the bark-beetle population in standing pine woods. It is stated that apart from abnormal increase brought about by exceptional breeding facilities as a result of fire, windfall, and felling operations, the conditions favouring the increase of bark-beetles and wood-boring insects in pine forests are considered to be mainly due to exceptionally favourable conditions for vigorous growth during the early stages of the crop's development, resulting in large numbers of trees being suppressed and killed in the pole stage, by rapidly increased shade as a result of the abnormal development of predominant trees. This is inevitable when Scots pine plantations are formed on soils too rich and situations too favourable. On the other hand, exceptionally favourable conditions for bark-beetle development occur when conditions are unfavourable for the healthy development of the crop owing to bad drainage conditions and water-logging of the soil.

6. The effect of overcrowding among the brood is considered to be one of the most important factors in the limitation of the bark-beetle population. Examples of how this factor operates are given and it is shown that the practical application of this factor can be brought about by the limitation of the supply of suitable breeding material.

7. The relative value of various parasites and predators as factors in the control of bark-beetles is discussed.

It is considered that pathogenic organisms are of little importance in the control of bark-beetles, as although these organisms may cause an epidemic when the pest has reached its maximum abundance, the object of our control measures must always be to prevent the bark-beetle population from approaching that stage of density.

Evidence is cited from the literature as to the effects of Nematode ~~worms~~ in reducing the egg-laying capacity of bark-beetles. It is suggested that the difference in the results obtained by various writers may have been influenced by the state of the insects at the time the observations were made, since the state of development of the reproductive organs of bark-beetles varies considerably during different stages, and although they sometimes appear to be shrivelled, they are capable of recuperation after a period of feeding. In any case it is impracticable to utilise Nematode worms in control measures, and it seems probable that their usefulness as parasites of bark-beetles will be neutralised by their effects upon the Coleopterous predators.

A list of the Hymenopterous parasites of pine beetles found during the progress of the investigation is given, together with notes on their relative abundance, and their importance as controlling factors is emphasized.

A list of the Coleopterous predators found associated with the bark-beetles is given with notes on the most important species. It is pointed out that some species of Coleopterous predators are probably more injurious than beneficial owing to the destruction of parasite larvae ; *Thanasimus formicarius* and Elaterid larvae are examples. On the whole, the Coleopterous predators are considered to be of even greater importance than Hymenopterous parasites as agents in the control of bark-beetles.

The larvae of several species of Diptera are very numerous in the bark-beetle brood-galleries. A list is given of the species which have been identified. Although listed as predators of bark-beetles, these Diptera are regarded as being of greater importance as destroyers of parasite larvae and are therefore being studied with a view to their possible elimination.

The economic status of birds in relation to bark-beetle control is briefly discussed, and it is pointed out that although under certain conditions birds do undoubtedly destroy large numbers of adult bark-beetles, it is probable that this useful work is counterbalanced by the destruction of parasite larvae in winter. On the whole, birds are not regarded as being of importance in the control of pine beetles in Britain.

The effects of competition between different species of bark-beetles is discussed, with special reference to *Crypturgus cinereus*, Hbst., and its influence in the control of *Myelophilus minor*.

8. A detailed description is given of some large-scale thinning experiments which have been in progress in the New Forest since 1933.

The scheme on which the experiments are based is the result of observations carried out by the writer over a period of years during which he noted that parasites and predators of the pine beetles are most numerous in young pine stands in the pole stage, previous to the first thinning operations. The conviction was formed that under those conditions a state of biological control existed which might, under favourable conditions, be continued throughout the rotation of the crop. One of the necessary conditions for the maintenance of a permanent resident population of parasites and predators is the presence of a permanent host population. This, in turn, necessitates a continuous supply of suitable breeding material. The density of the host population is largely governed by the quantity of suitable breeding material available, and the requirements of an increasing bark-beetle population demand a corresponding increase in the amount of suitable breeding material from year to year ; so long as this increase in suitable breeding material continues, the host population is maintained at a higher level than that of the parasites and predators. When, however, the supply of suitable breeding material ceases to meet the requirements of the increasing bark-beetle population, a point is reached where overcrowding of the brood takes place. The intersection and intermingling of the larval tunnels facilitates the work of destruction by the predator larvae and the balance is, for a time, turned in their favour. The increased density of the host population also favours the increase of the parasites at the expense of the host. Limitation of the supply of suitable breeding material also results in a high rate of mortality among the bark-beetle larvae. The combined effects of the increased parasite and predator population, accompanied by overcrowding in a limited supply of food material, will result in a sudden reduction in the bark-beetle population, which is followed by a corresponding reduction in the parasite and predator populations. It will be seen, therefore, that under natural conditions there is a considerable fluctuation in the rise and fall of the numerical ratio of the host population and that of the parasite and predator population. The time occupied by each cycle may be extended over a considerable period of years, the peak of each host infestation giving rise to a periodic outbreak, corresponding with the period of maximum density of the crop. The automatic opening up of the canopy results in a temporary reduction in the amount of suitable breeding material. Under silvicultural conditions, however, the sudden increase of available breeding material produced when a thinning takes place and the material is allowed to remain on the area provides abnormally favourable conditions for the sudden increase of the bark-beetle population, and an outbreak is precipitated. The occurrence of these outbreaks has led to the popular belief that the remedy lies in what is called " clean forestry." In theory, the elimination of all suitable breeding material would solve the bark-beetle problem, but in practice the method is often impracticable when large areas of forest have to be dealt with, as is clearly demonstrated by the frequency with which bark-beetle outbreaks occur as a result of thinning operations.

The object of the experiment was, therefore, to devise a method by which the state of biological control can be continued throughout the rotation, by the provision of the amount of breeding material necessary to maintain a permanent population of hosts which would be kept at a level of economic control by the parasites and predators, and at the same time to bring into practical application the factor of overcrowding as an automatic governor to check any undue increase of the bark-beetle population. The results of the experiments are given in detail, and it is shown that the rate of growth of the crop is a decisive factor.

A scheme is outlined for the study of the use of billets and trap-stems.

Reference is made to operations which tend to upset the balance of insect populations.

Control measures in felling, burnt, and windfall areas are also discussed.

Acknowledgments.

The writer is indebted to Dr. W. R. Thompson, F.R.S., for allocating the task and for helpful co-operation and encouragement throughout the work of the investigation ; to the Forestry Commission for the many facilities afforded ; to Mr. D. W. Young, M.B.E., Deputy Surveyor of the New Forest, for much help in implementing the work ; to Mr. J. M. B. Brown, of the Imperial Forestry Institute, for assisting with some of the experiments ; to Dr. C. Ferrière for the determination of the Hymenoptera ; to Sir Guy A. K. Marshall, C.M.G., F.R.S., for the determination of the Diptera ; to Dr. K. G. Blair for assistance with the Coleoptera ; to Dr. S. A. Neave, O.B.E., and the members of the staff of the Publication Office of the Imperial Institute of Entomology for much valuable assistance in translating the Continental literature ; and to Mr. R. J. Spittle for copying the tables and diagrams.

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EXPLANATION OF PLATE VI.

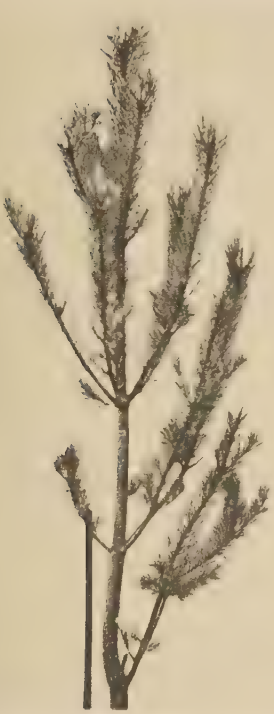
Fig. 1.—Shows four years' growth subsequent to the loss and replacement of a leading shoot. In this case the defect is not very serious.

Fig. 2.—The formation of a " kink " or " bayonet " in the stem of a young tree, caused by the destruction of the original leader and all the shoots on the uppermost whorls of branches. Replacement of the leader has taken place from a branch at a lower level, with a considerable loss of height growth.

Fig. 3.—A " kink " or " bayonet " formation in the stem of a Scots pine tree. This makes the tree unsuitable for use as a telegraph pole.

Fig. 4.—A " fork " caused by the destruction of the leading shoot and the whole of the shoots on the uppermost whorl of branches.

PLATE VI



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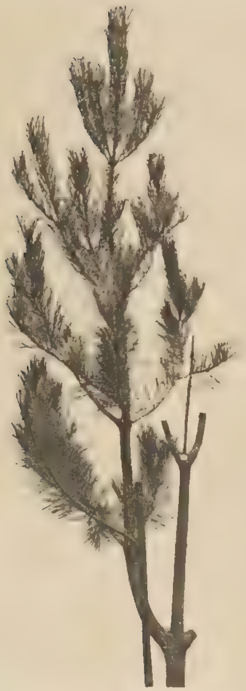

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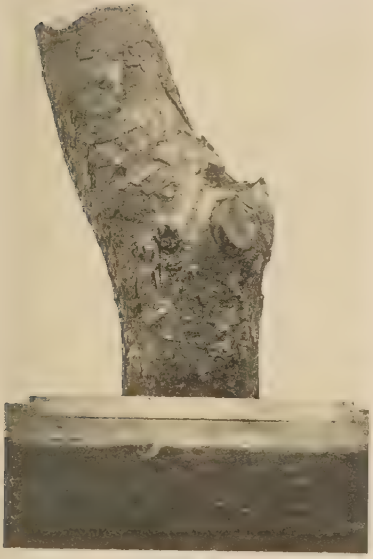

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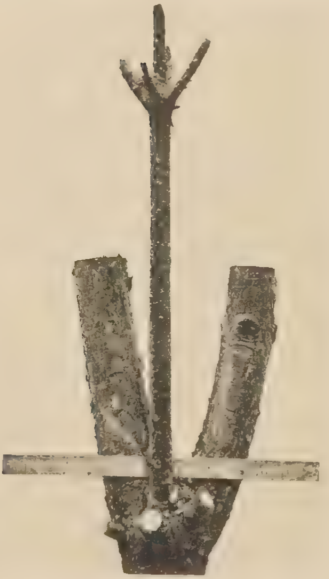

Fig. 4.

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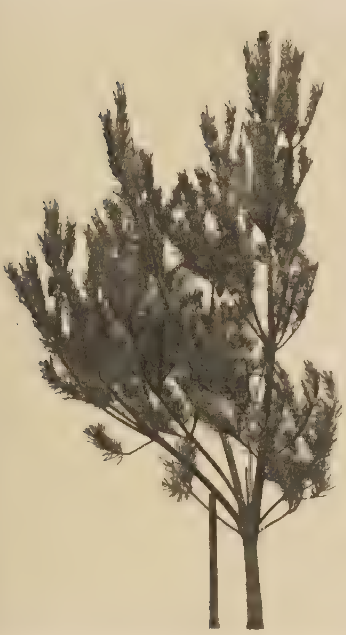
EXPLANATION OF PLATE VII.

Fig. 1.—The development of a " wolf " tree, caused by several new leaders arising as the result of the loss of the leading shoot in a vigorously growing young tree. The remains of the original leader may be seen in the centre of the whorl immediately above the main axis of the stem.

Fig. 2.—A section of a triple crowned tree caused by the loss of the leading shoot in a vigorously growing young tree.

Fig. 3.—A " bayonet " formation in the stem of a standing tree.

Fig. 4.—A " spire top " caused by the destruction of the whole of the terminal and lateral shoots. The result of repeated attacks on the crown of a tree in the pole stage.



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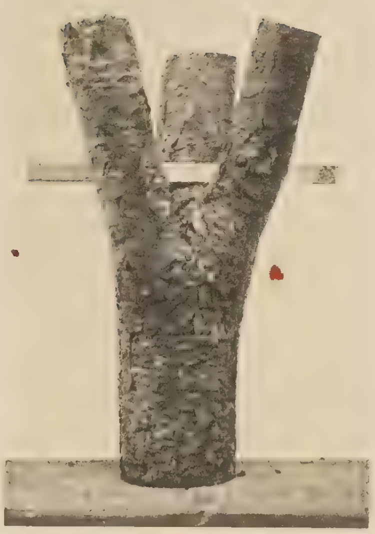

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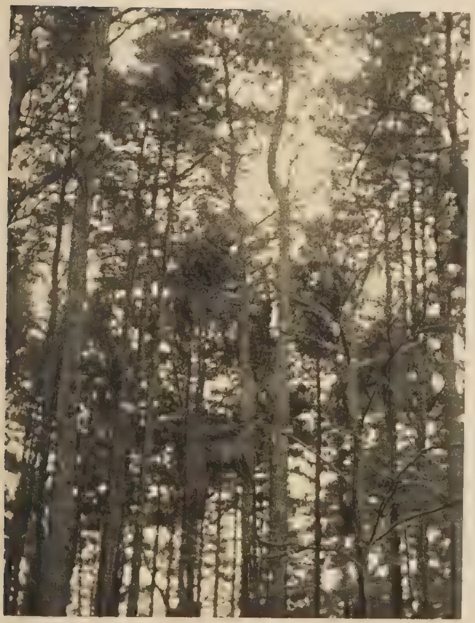

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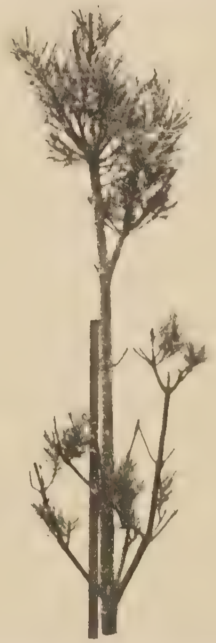

Fig. 4

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EXPLANATION OF PLATE VIII.

Fig. 1.—Part of a belt of Scots pine trees with "spire tops." The result of repeated attacks by *Myelophilus*.

(N.B.—In this figure some of the "spires" have been omitted.)

Fig. 2.—Part of the base of the stem of a sixty-year old Scots pine tree, showing boring meal or "frass." The result of *Myelophilus* adults "winter feeding" in the bast.

Fig. 3.—Pine shoots destroyed by *Myelophilus* during the process of "regeneration feeding" on the crowns of standing trees. The average density of the fallen shoots in this case was 128,520 per acre.

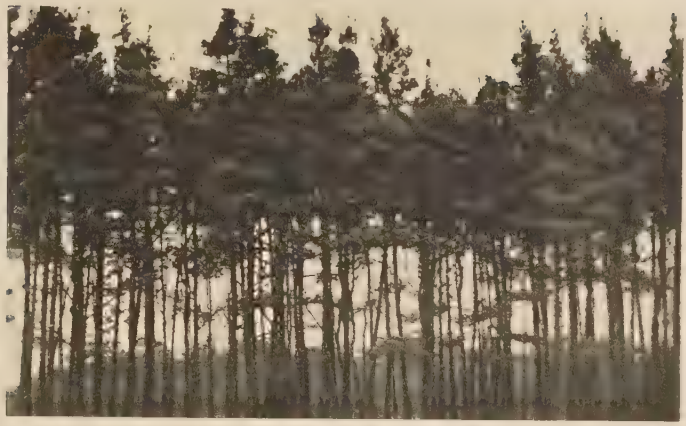

Fig. 1

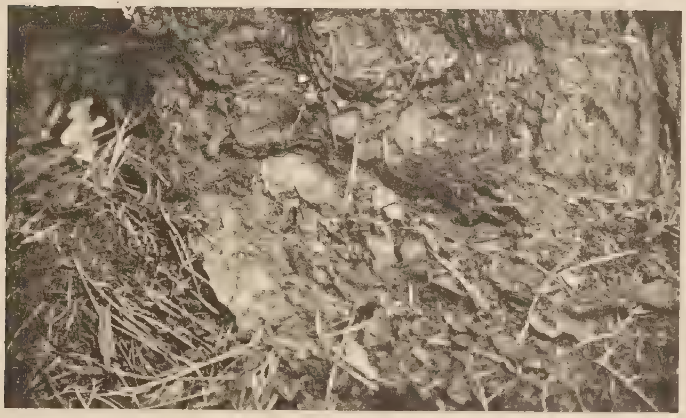

Fig. 2

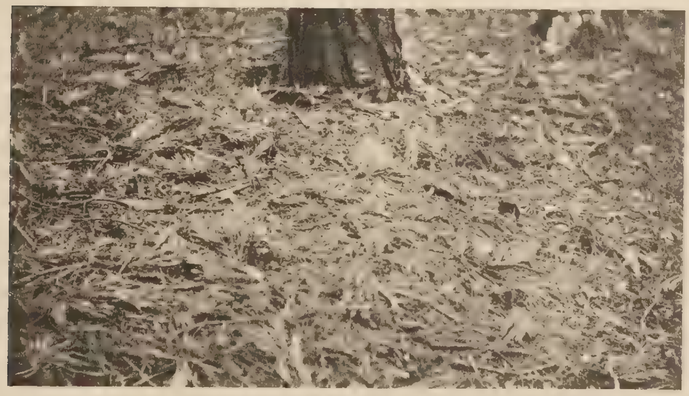

Fig. 3

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A STUDY OF SPONTANEOUS LOCOMOTOR ACTIVITY IN *LOCUSTA MIGRATORIA MIGRATORIOIDES* (R. & F.) BY THE ACTOGRAPH METHOD.

By E. Berry Edney, Ph.D., B.Sc., D.I.C.

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Introduction.

Since the general acceptance of Uvarov's Phase Theory of Locusts, investigations have been concentrated on discovering what factors bring about a change from one phase to the other. Plotnikov (1924) and Faure (1923), working separately, showed that density of population was the factor concerned. Climatic factors such as light, temperature and humidity were found to have no effect by themselves, though it was demonstrated that variations in these factors did increase or decrease the effect of crowding.

Uvarov (1928) put forward the view that the amount of gross bodily activity was the factor which determined the phase of an insect and that it was by bringing about a high activity that the density of population had its effect.

Faure (1932) in an important paper further investigated this matter, and showed that intensity of activity was indeed the phase-determining factor.

Quantitative data on the activity of the locust or of any insect are scarce, and it appears to be of importance that these should be available if our knowledge of the exact mechanism of phase transformation is to progress.

In all work where the effect of changes of conditions on activity is being considered, it is of the greatest importance that the normal or "spontaneous" activity and variations in activity of the animal being studied should be known.

If an investigator is not in possession of such data, a variation which is normal and which would occur under constant conditions may be erroneously attributed to an experimental variation in conditions. The present study is an attempt to provide quantitative data concerning the amount of activity which is shown by a locust at different stages of its life, the amount of variation which must be expected, and the effect of varying certain conditions. The type of activity considered is voluntary or spontaneous locomotor activity and it is measured in terms of distance travelled in 24-hour periods. This simple method of expressing activity is considered to be quite suitable for the purpose required, that is, as a medium for making comparisons and expressing variations.

In view of the many different meanings which the word " activity " can convey, it may be stated here that " activity " in the following is used to mean " gross bodily activity " except when otherwise qualified.

Material.

The material used in the present work was obtained from a stock of *Locusta migratoria migratorioides* (R. & F.) from Central Africa, which had been bred for over ten generations in the locust laboratory of the Imperial Institute of Entomology, London. A special stock was bred for the purpose of the experiments to be described. The insects were kept in a large metal and glass cage in the laboratory and during the course of the work have been bred through seven generations.

Insects to be used for experimental purposes were removed from the breeding cage as soon as they hatched and placed singly in jars in a constant temperature room, in which all experiments were done. The temperature in the C.T. room remained constant at 27°C., the greatest daily variation being 0·5°C., and the average about 0·1°C. The insects were kept in small jars covered by glass plates during the first instar, as it was found that they needed a higher relative humidity than in other instars. After moulting to the 2nd instar each insect was placed by itself in a cage 8 ins. high by 6½ ins. by 6½ ins. The bottom of each cage was made of three-ply wood ; the sides were of glass held together at the corners by adhesive paper, and the top consisted of a lid of perforated zinc.

Twenty such cages were made, so that it was possible to keep twenty insects for experimental use. Each insect was given a number and a record was kept of all the relevant factors in its life, such as dates of moults, date of death, abnormalities, etc. Grass was fed to each insect each day ; this was placed in a small tube of water on the floor of the cage ; it was found that the grass remained satisfactorily fresh for a day and lasted if necessary for two days. Each cage was cleaned once a day at feeding time.

It is clear that under these conditions only insects of phase *solitaria* could be developed, and this was borne out by the colour of the hoppers and the measurements of the adults. Twenty insects were measured to the nearest 0·1 mm., using a mm. scale. The average for the 20 insects of the ratio " length of elytra to length of hind femur " was 1·79, the maximum 1·92, and the minimum 1·67.

The light intensity varied in different parts of the room, which was lighted continuously by gas-filled bulbs. It cannot, therefore, be claimed that each insect was subjected to exactly similar light conditions, but all the cages were placed so far as possible in well lighted positions and the light intensity was certainly constant for individual insects.

The relative humidity in the C.T. room varied from 35 per cent. to 45 per cent. at different times of the year, the average daily variation being about 2 per cent. The instrument used for measuring humidity, wherever it is mentioned, was the " Edney " paper hygrometer, and the method of calibrating these instruments has been described fully by Key (1936 *a*).

The humidity varied in different parts of each cage from 40 per cent. to 63 per cent. There was, therefore, a considerable humidity gradient, but it was noticed that the insects usually rested either on the grass or in the damper parts of the cage.

The humidity during the conditioning of an insect for experiment cannot, therefore, be said to have been constant, but it is reasonable to assume that the insect would spend most of its time in the humidity which was nearest to its optimum and thereby tend to minimise the variations.

Apparatus and Technique.

The apparatus used for recording automatically the locomotor activity of the insects was constructed on the principle of Szymanski's Actograph. It consists (fig. 1) of a light aluminium beam (B) supported in the middle by a knife-edge (K) resting on a hard metal plate. At one end of the beam a cage (C) can be attached, and to the other end is fixed a writing point (P) which makes contact with the smoked surface of a record paper on a revolving drum (D). The drum used was 6½ ins. high, with a circumference of 16½ ins., and revolved once in 24 hours. The beam is then free to swing in a vertical plane and its position at rest can be adjusted by moving the sliding weight (W).

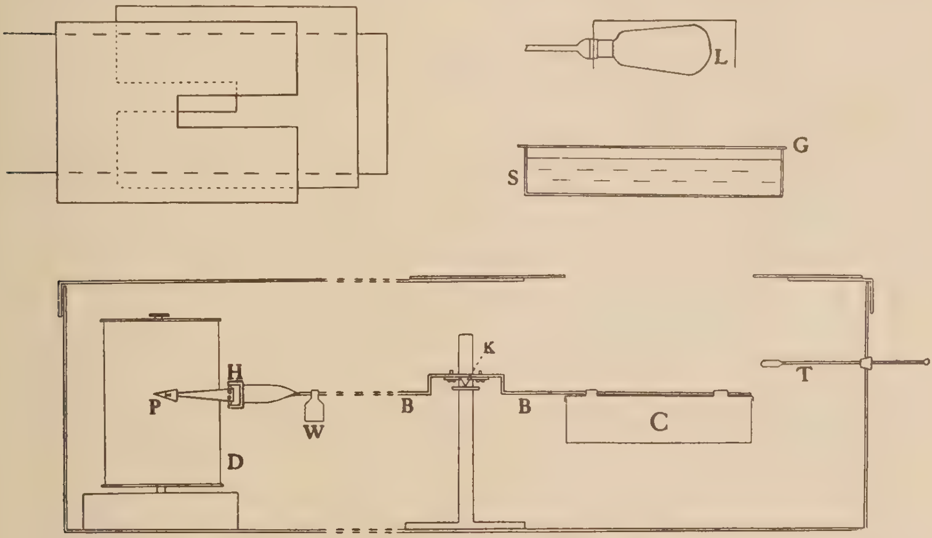


Fig. 1. Actograph apparatus, and arrangement for regulating light opening in box. B. Beam ; C. Cage ; D. Revolving Drum ; G. Frosted Glass ; H. Hinge ; K. Knife-edge ; L. Light ; P. Writing Point ; S. Water Screen ; T. Thermometer.

Now if an insect be introduced into the cage, as it travels up and down, a vertical line is drawn by the writing point on the smoked paper, and when the insect is at rest a horizontal line is drawn as the drum revolves.

The cages used with this apparatus, termed "activity cages," were made of "celastoid," a light transparent material similar to celluloid. A different-sized cage was used for each stadium ; the adult activity cage was 9 ins. long by 3 ins. deep by 2 ins. wide ; the lengths of the cages used for the other stadia were : 5th instar, 8 ins. ; 4th instar, 6 ins. ; 3rd instar, 4 ins. ; 2nd and 1st instars, 8 cm. ; and the other dimensions in proportion. Cages of this shape provided ample room for the insect to travel backwards and forwards in the direction of the beam, movement in which direction would be recorded on the drum, but no room for the insect to spend much energy in travelling from side to side, which movement would not be clearly recorded.

On the inside of the bottom of each cage a piece of fine muslin was gummed in order to provide a satisfactory foothold for the insect. Similarly a different-sized beam was used for each instar, varying in length from 28 ins. for the adult to 8 ins. for the 1st and 2nd instar hoppers. The cage was attached to the beam by two celastoid " bridges " on the lid, and two rubber bands.

Care had to be taken to ensure that conditions as nearly constant as possible obtained when an insect was in an activity cage. The whole apparatus was therefore enclosed in a large cardboard box painted a dull black inside. The sides and bottom of each activity cage were covered with black paper so that light could enter only from the top. The source of light was a 70-watt pearl electric light bulb (fig. 1, L), 26 ins. from the top of the activity cage when in a horizontal position. Between the light and the box was a water-screen (S) and a frosted glass plate (G). This was found to be necessary, as the temperature inside the box otherwise rose three or four degrees when the light was switched on. The light was admitted to the box through a large rectangular opening 18 ins. by 10 ins. in the lid. It was desired that there should be no directional stimulus influencing the insect in the activity cage, therefore it was necessary to admit the light directly from above only. This was arranged by using two large pieces of cardboard each with a rectangular indentation at one edge of a similar shape and size to the bottom of the largest activity cage (9 ins. by 2 ins.). It will be readily seen by referring to fig. 1 that by adjusting these pieces of cardboard, an opening of any desired size up to the size of the largest cage could be obtained.

The temperature was kept constant by placing the whole apparatus in a constant temperature room at 27°C. A thermometer (fig. 1, T) held by a cork in a hole through the cardboard box was used at first and readings were taken before, during and after experiments, but as the temperature was found to remain constant at 27°C. the practice was discontinued.

The type of record obtained from this apparatus is shown in fig. 16, A (*a*), where a schematic representation of the record is also given. The method of constructing such diagrams will be described later.

To ensure correct interpretation, a number of observational records were taken of all stages. Each observation record lasted for from three to four hours, and it was found that a very close correlation existed between the actograph record and the detailed notes made of movements.

It was noticed during these observational records that almost all the activity was expressed as motion along the long axis of the cage. When the insect came to one end the usual procedure for turning was to rear up in one corner and slide down in the other. In this process the insect does expend a certain amount of energy which is not recorded as activity. However, the proportion of the total energy unrecorded in this way is small and is the same for all the insects, and as the greater part of the experimental results consists of comparisons between the activity of the same individual at different times or of different individuals, this small proportion of unrecorded activity has been neglected.

It was also noticed that the bare celastoid sides were quite effective in keeping the insect on the floor of the cage. As it moved along the side, the front leg nearest the wall was from time to time raised as if to start climbing up, but as no hold at all was obtained, it simply slipped down to the floor and the insect proceeded forwards.

Two complete sets of apparatus were made ; records made, using the first apparatus, were numbered from 1 to 346, and were taken nearly continuously from March 1935 to May 1936. Records on the second apparatus were numbered A.1 to

A.283, and were taken from June 1935 to May 1936. Each record, except where otherwise stated, represents the locomotor activity over a period of 24 hours.

The method used for expressing the amount of activity was as follows:—The length of a vertical stroke representing a full journey from one end of the cage to the other is easily judged, as the majority of strokes are of this length and the record thus takes the form of a band of constant width. The number of complete strokes shown on the record was then counted, considering half strokes as such, strokes more than half as full strokes, and neglecting strokes less than half the maximum amplitude. This total then represents the number of times the insect has travelled from one end of the cage to the other. As each record represents 24 hours and the drum has a circumference of 16½ ins., a distance of roughly two-thirds of an inch on a record represents an hour. If a sufficiently fine writing point is used, as many as sixty strokes an hour can be recorded with sufficient clarity to allow of an accurate count, and the locomotor activity under the conditions which obtained during the experiment was very seldom of a higher intensity than this.

The number of strokes in each record was counted from the beginning, that is, no allowance was made for acclimatisation, as the records showed that adjustment to environment was very rapid, indeed the majority of records commenced with a rest period.

The feeding of the insects during the course of a 24 hour experimental period had to be considered, as it was not known what effect hunger might have upon the amount of activity shown. It was found to be impossible to keep an insect constantly supplied with fresh food during the whole 24 hours in an activity cage. It was decided, therefore, to give each insect a weighed quantity of fresh grass at the beginning of each record, and so for each stadium a quantity constant for all individuals of that stadium was given. The quantities were as follows: Adults, 1 gm., 5th instar, 1 gm., 4th instar, 0·5 gm., 3rd instar, 0·35 gm., 2nd instar, 0·2 gm., 1st instar, 0·1 gm. The grass was cut into pieces about ¼ in. long and spread evenly over the floor of the activity cage.

This method of feeding ensured that there was a similar environment as regards food for all insects. This environment, however, was not constant over each 24-hour period, as it was found that the grass not eaten by the insect at the end of a record was quite dry. So that for a certain part of the record there had been fresh food for the insect and for the remainder of the period the grass had become unpalatable. The moisture content of samples of grass on different days varied very little. Of thirty such measurements the average moisture content was 76·2 per cent. by weight of the weight of fresh grass. The standard deviation from the average was 4·4 per cent., which is a relatively small variation and consequently negligible.

Observations were also made to determine after what period in the 24 hours the grass in the cage became unpalatable to the insect. The quantity of fresh grass, appropriate to the size of the cage used, was left to dry in the cage for different periods of time. It was then presented to an insect which had been kept away from food for a similar period of time and it was noted whether the insect started to eat or not in the first five minutes. Twenty such observations were made, using both adults and nymphs, and it was found that in no instance was grass which had been allowed to dry for more than 13 hours eaten (five observations). Grass which had dried for 12 hours or less was taken in 5 out of 6 trials, and of the remaining 9 trials, between 12 and 13 hours drying, the grass was taken in five and refused in four. The conclusion to be drawn from this was that the grass became unpalatable after about 12½ hours in an activity cage. For the sake of simplicity, and for other reasons indicated below, it was considered that the insect whose activity was being recorded had food in the first half of a record, but not in the second half.

The experiments are not described in the order in which they were carried out, neither were they done in any strict sequence, owing to the scarcity or lack of insects of the appropriate stage of development at the required time. Further, an opportunity was taken whenever it occurred of obtaining extra records to substantiate those already obtained. However, as all the records were numbered consecutively, these numbers are an indication of the position of any one record in the series.

It was found in practice that records of the activity of 1st instar hoppers were difficult to obtain. The very small weight of these insects was scarcely enough to overcome the friction between the writing point and the smoked paper, even though the activity cage and beam used were as light as possible. Although many attempts were made to obtain 1st instar records, only 10 were clear enough to allow an accurate count to be made, so that only a few figures can be given concerning this stadium.

The Variation in Amount of Spontaneous Activity.

A few preliminary records were taken to obtain an idea of the type to be expected, and the point which first emerged was the very great variation in amount of activity shown by different individuals and by the same individual on different days. The experiments in this section were designed to investigate this variation, whether it is entirely at random, or whether there is any correlation between the level of activity and the stage of development.

(*a*) *Nymphs.*

It was decided to measure the variation in amount of daily activity over each stadium. Consecutive records were therefore taken of an insect from the time it moulted to one instar, until it moulted to the next. Records of the activity were obtained of at least four insects, two of either sex, through each stadium.

As the insects were fed and records set up once a day, it was not always possible to know the exact time at which an insect moulted. Feeding took place usually about mid-day, so that if an insect was seen not to have moulted, when fed on one day, and to have moulted when fed the next day, the time of moulting was taken to have been at midnight between the two days. Successive 24 hour records were then taken of the insect's activity and the time noted when the moult to the next stadium occurred. This could be determined from the activity record, as will be shown later.

The length of any given stadium in days, varied very considerably between different individuals. For the purpose of comparing the variations in the level of activity shown by different individuals during the course of a stadium, the time taken by any individual to complete the stadium was taken as 100, irrespective of the actual time, and the proportion of the stadium passed through by the insect concerned at the beginning of each record was expressed as a percentage of the total time taken to complete the stadium. This meant, more simply, a stretching out or a shortening of the length of a stadium in order to bring the times taken by different individuals to a common level.

It will be seen that this method possesses the further advantage of making it possible to compare the variations of activity over one stadium with another.

A selection from the figures obtained from these records (Table I) shows the very high degree of variability.

The figures in the columns showing " Activity in strokes " represent the number of strokes in each 24 hour record and the corresponding figures in the columns " percentage of development passed " show the proportion of the stadium which the insect has passed through at the beginning of the record concerned.

The conditions of light and heat were constant throughout, but each 24 hour record represents 12 hours with food and, consequently, a high humidity, and 12 hours without food, and with a low humidity.

TABLE I.

Variation in Daily Activity of one Male and one Female over the 5th Stadium.

Record number	Insect number	Sex	Percentage of development passed	Activity in strokes
A80	163	Female	0	3
A81	,,	,,	7	63
A82	,,	,,	14	168
A83	,,	,,	22	104
A84	,,	,,	30	226
A85	,,	,,	37	758
A86	,,	,,	44	98
A87	,,	,,	52	235
A88	,,	,,	59	720
A89	,,	,,	67	50
A90	,,	,,	74	95
A91	,,	,,	81	11
A92	,,	,,	89	22
A93	,,	,,	96	34
256	221	Male	0	67
257	,,	,,	7	24
258	,,	,,	15	80
259	,,	,,	22	270
260	,,	,,	29	120
261	,,	,,	37	51
262	,,	,,	44	334
263	,,	,,	51	195
264	,,	,,	59	30
265	,,	,,	66	168
266	,,	,,	74	125
267	,,	,,	81	31
268	,,	,,	89	5
269	,,	,,	96	90

The same quantity of fresh grass was given to all individuals of any one instar, and as has been shown above, the moisture content of this grass varied very little. It was therefore assumed that although conditions of food and humidity varied over the 24 hours, they did so in a manner similar for each insect. If this assumption is made, then a comparison can still be drawn between the amounts of activity shown at different times even though the amounts are abnormal in so far as the conditions of hunger fluctuated. It will be shown later that the fluctuation in relative humidity had little or no effect.

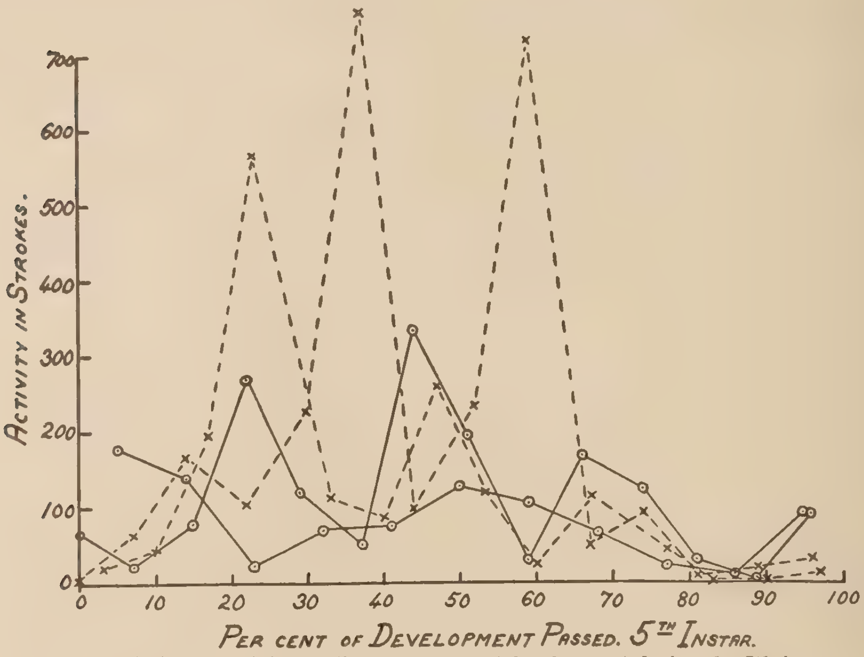


Fig. 2. Variation of activity at different stages of development during the 5th instar. Unbroken line, males : broken line, females.

The results of this experiment are more easily appreciated in graphical form. Fig. 2 is such a representation of all 5th instar insects, and does not differ essentially from the results for other stadia. Points representing the activity of one individual at successive stages of development are joined, but these lines must not be taken to represent a continuity in the levels of activity. Each point represents the amount of activity occurring in the 24 hours after the position of that point along the time scale.

These figures for each stadium show a very great variation in the amount of activity. The only common feature appears to be a higher level of activity in the middle than at the beginning or end of a stadium. In order to correlate the figures for all individuals and bring out the correspondence in a more demonstrable form, it was decided to take the figures for each individual separately and to express each as a percentage of the maximum for that individual. In this way all the curves could be brought to a common level and their correspondence studied.

The figures for each instar, having been expressed each as a percentage of the maximum of the individual concerned, were then divided into ten sections according to percentage of development passed and an average of each section taken.

This method is, in effect, simply a reducing of the maximum activity shown by all individuals to a common level in order to find if there is a feature common to all in the way the amount varies over a stadium.

The figures treated in this manner are shown in Table II, and fig. 3 expresses the results in graphical form. Histograms were obtained in this way for all instars and several points of similarity emerged. Each shows a peak at about 50 per cent. of development passed, and a rapid falling off after this peak to a very low figure between 80 per cent. and 90 per cent., and a sharp increase between 90 per cent. and 100 per cent. This last point will be discussed later.

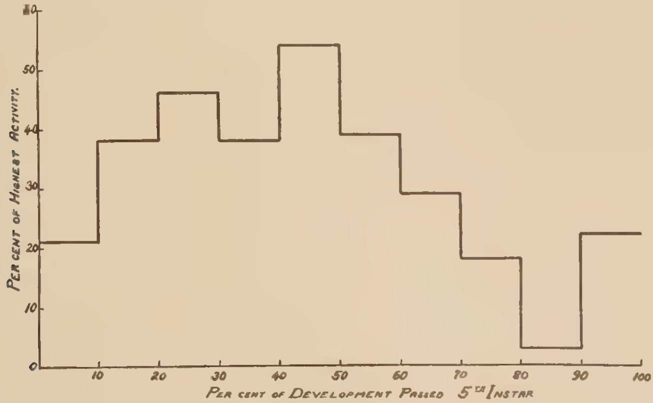


Fig. 3. Variation of activity during the 5th instar. Average of all individuals.

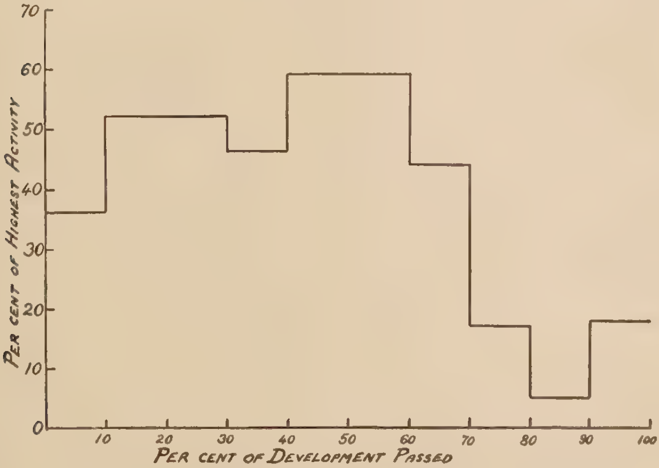


Fig. 4. Variation of activity ; average of all stadia and all individuals.

If the figures in each of these 10 per cent. divisions are averaged for all the instars studied, the above points of resemblance still appear (fig. 4). There is a peak from 10 per cent. to 30 per cent., a higher peak from 40 per cent. to 60 per cent., then a rapid fall, followed by a sharp rise, between 90 per cent. and 100 per cent.

Only 17 individuals were determined throughout a stadium, so that only the most general statements can be made concerning the fluctuation of activity over a stadium. All that can be said, then, is that the highest level of activity can be expected at about half-way through a stadium, and that the level falls off on either side of this, to a lower level at the end of a stadium than at the beginning.

TABLE II.

The Fluctuation of Amount of Activity over each Stadium.

Instar	Percentage of development passed									
	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100
2 ...	30	43	35	53	100	70	46	20	1	4
3 ...	61	54	44	40	56	100	44	10	12	20
4 ...	44	70	79	60	49	67	63	19	7	20
5 ...	21	59	46	38	54	39	29	18	3	22

Average for all insects of percentage of highest activity shown by insect concerned.

It will be convenient to discuss at this stage the occurrence of the sharp increase of activity in the last 10 per cent. of development of each stadium. This high activity always occurred in the last of the series of records taken over the course of a stadium and was further concentrated into one fairly short period of activity, which formed a striking contrast with the remainder of the record before and after, showing as it did almost complete rest. The period of high activity was found by observation to be associated with the process of moulting. A 5th instar nymph which was very near the point of moulting was placed in an activity cage and a record taken of its activity. At the same time frequent observations were made of the insect. It was found that continuous high activity was shown for an hour before the process of moulting began. This lasted for 20 minutes, after which there was activity for a further 15 minutes, and the remainder of the record, taken for six hours, showed rest.

It would appear then, that for some time before a moult occurs the insect seeks a convenient moulting place, usually a projection from which it can hang head downwards, but that if such a place is not discovered, it is capable of showing a high intensity of locomotor activity until the process of moulting is over.

All the available records during which a moult occurred are shown diagrammatically in fig. 5. The method used of representing actograph records schematically is as follows :—Four activity grades are used, a black period represents high activity of over 20 strokes per hour, single lines close together represent activity between 8 and 20 strokes per hour, activity of a lower intensity than this is represented by isolated lines, each line representing one stroke, and for complete rest the diagram is left open.

It will be observed in each of these diagrams (fig. 5) that apart from one main period of activity the insect spent most of the time at rest. The moult in each record can be said to have occurred some time during the last hour of the chief period of activity, and as is shown by the diagrams (fig. 5), this can occur at any time during the 24 hours. Since each of the insects, records of whose moults are shown in the figure, have had alternating periods of 12 hours with food and 12 hours without, during the previous stadium, it can be said that such a regular recurrence of feeding periods does not influence the time at which the moult occurs.

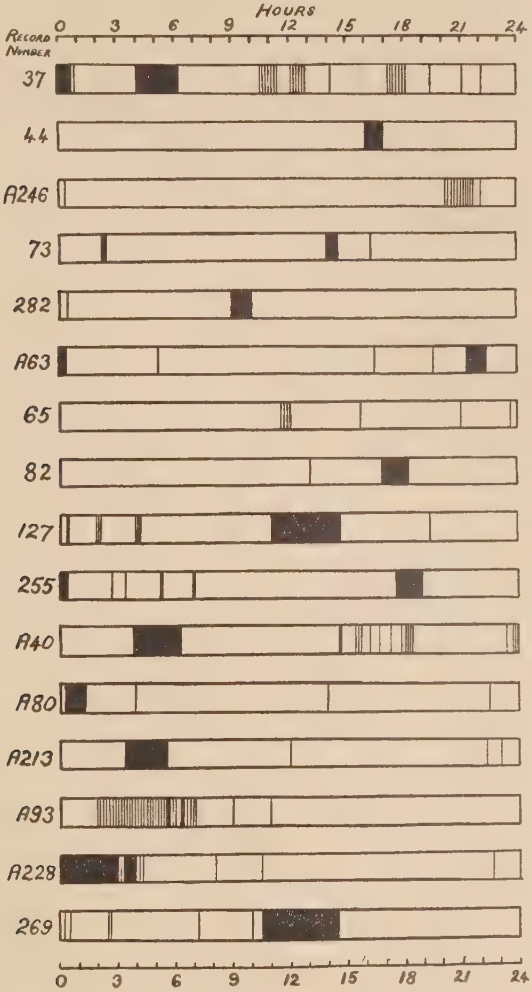


Fig. 5. Schematic representation of records during which moults occurred.

2nd–3rd Instar :	37–A246
3rd–4th ,,	73–A 63
4th–5th ,,	65–A213
5th Instar–Adult :	A93–269

(*b*) *Adults.*

The figures obtained for the daily activity of adults are summarised in Tables III and IV. Table III shows the activity of adults up to seven days old, the average figures showing an increase up to the fifth day. That there is an increase in the first few days is clear, but owing to the small number of insects determined (three of each sex) it is difficult to say accurately for how many days the increase continues. Further, the increase shown by any one individual is not entirely regular and the length of time during which the increase continues varies from insect to insect, so that an average figure for this period is of little use ; all that can be said is that for each adult insect an irregular increase in daily activity can be expected, continuing for about five days.

The daily activity of two adults, one male and one female, was recorded for as long as they lived. The figures so obtained are summarised in Table IV and refer to the daily activity after the insects were seven days old. The female lived longer than the male, 74 days as compared with 64 ; the last two days' activity in each is not taken into consideration in Table IV, as during this time the insects were dying and the activity decreasing.

TABLE III.

Activity of Adults for first 7 Days.

Insect no.	Sex	Days old						
		1	2	3	4	5	6	7
			Activity in number of 9-inch journeys per day.					
163	F	3	21	28	27	112	125	79
67	F	—	45	137	162	144	109	63
108	F	39	71	95	168	143	153	178
114	M	26	59	41	57	71	93	102
78	M	—	221	—	—	184	104	24
218	M	60	150	96	160	184	203	133
Average ...	...	32	93	79	115	140	131	96

TABLE IV.

Activity of Adults over 7 Days old.

Insect no.	Sex	No. of records	Mean daily activity	S.D.
163	F	61	68	45·3
114	M	54	78	32·5

There is no statistical significance in the difference between male and female, for such a difference would occur 1 in 4 times if due entirely to chance.

The mean daily activity of the male locust studied was higher than that of the female (78 strokes as compared with 68), but the variations in the daily total of each were large, as is shown by the Standard Deviation, 45·3 in the female and 32·5 in the male. The difference between the male and female activity was tested statistically, using the method described by Fisher (1934), and found not to be significant ($p = 0{\cdot}7$). Such a difference would occur once in every four times if the figures were due entirely to chance.

No difference was observed in the amount of daily activity before and after sexual maturation. The exact time after emergence at which sexual maturity was reached under the conditions in the C.T. room is uncertain. According to the figures given by Hamilton (1936), maturation would take place very slowly under such conditions and the variation between individuals would probably be considerable.

(*c*) *Comparison of the activity at different stages of development and in the two sexes.*

The simplest method of comparing figures representing the type of activity measured in the present work is to compare the average distance travelled in a given time. Therefore, in order to compare the activity shown by the different stages and the sexes, an activity figure was calculated for each stadium in the following manner :—

The figures obtained from records of each stadium were first brought to a common basis by expressing each in terms of distance travelled. Each stroke in a 4th instar record represents a journey of 6 ins. ; by multiplying the number of strokes in other instars by the appropriate factor these were also reduced to represent the number of 6–inch journeys.

Now the level of activity has been shown to vary considerably during the course of a stadium, so that in order to include all the available records it was necessary to allow for the stage of development in a stadium at which they were taken. The figures were therefore classified into 10 sections as before, according to the percentage of development passed through at the beginning of the record. This was done separately for the males and females and for each instar and the average taken for each 10 per cent. division. The figures thus obtained for each 10 per cent. division were added for the whole stadium and the average again taken. This gave the "activity figure" for the instar concerned and represents the average number of 6-inch journeys made by an insect in 24 hours. The results are given in Table V.

The figures show that of the insects studied the females travelled further than the males in instars 2, 4 and 5, but the males travelled further in the 3rd instar. A statistical examination of these results, however, again showed that the difference was not significant (p = 0·6).

TABLE V.

Instar	Activity figure *		
	Males	Females	Average
2	42·4	54·1	48·2
3	50·4	28·3	39·3
4	114·8	192·2	153·5
5	137·3	214·5	175·9
Average	88·2	122·3	—
Adult ...	120·0	96·1	108·0

The difference between males and females (hoppers) is not statistically significant.

* For the method of obtaining the activity figures in this Table, see text.

Comparing the instars irrespective of sex, we find there is an increase in the average distance travelled in 24 hours from the second to the fifth instar, except for the third, which is rather lower than the second. Bodenheimer (1930) in his studies on the rate of progression of hoppers of *Schistocerca gregaria*, found that the maximum speed of progression, which was reached at about 30°C. (only three degrees above the temperature at which the present experiments were conducted), was the same for all instars, and that hoppers of all stages took part in the mass movements, the small ones keeping up with the big ones without apparent difficulty. However, it must be borne in mind that whereas the small hoppers in a mass movement are continuously receiving strong external stimuli, the hoppers used in the present work were kept as free from all such stimuli as possible. It may be that the amount of spontaneous activity shown by young hoppers is, indeed, less than that shown by older ones, but that if they are subjected to very frequent external stimuli the amount of locomotor activity is thereby increased to that of the older hoppers.

The figures for the adult stage included in Table V could not be taken into the average, as they were not obtained in precisely the same way as were those for the nymphs. They are derived from the figures in Table III. The figures were first reduced to represent the number of 6-inch journeys made, then an average was taken (*a*) for males, and (*b*) for females, of the daily activity for each day, and finally an average was taken of the first seven days' activity. The average figure for both sexes, which represents the average number of 6-inch journeys made by an adult locust up to seven days old during a period of 24 hours, can be compared with the corresponding figures for the nymphs. The average for those insects determined was 108 6-inch journeys, a figure lower than that for either 4th or 5th instar insects.

The results obtained by Key (1936 *c*) on this subject were rather different from the present set. He found the average distance travelled by females in a half-hour period was less than that for males, a difference of 19·8 per cent. in insects kept wet, and 5 per cent. in insects kept dry, whereas the result of the present work is that there is no significant difference. Key remarks that his figures only suggest that there is a difference between the activity of the sexes, and it appears probable that if his figures were tested statistically the difference would be found not to be significant.

Distribution of Activity over 24 Hours.

So far we have been considering the distribution of activity in relation to stage of development and expressing the results in terms of the distance travelled in 24-hour periods. We come now to a consideration of the distribution of activity within the 24 hours. The few preliminary records previously mentioned all agreed in showing more activity in the second half than in the first. This increase in the second half might be an indication of a diurnal periodicity or due to a change in the internal or external environment of all insects during each 24-hour period.

All the insects used had been kept in the C.T. room, so that there had been no diurnal fluctuation in their previous environment. However, other workers (Szymanski, 1914, 1918, 1920, Keeble, 1910, Wolf, 1930, and Von Stein-Belling, 1935) have shown that animals may retain various diurnal periodicities for a long time after the removal of the environmental conditions inducing the periodicity.

To determine whether such a diurnal periodicity existed in the locust, records of all stages were taken, beginning at different times of the day; at 10.0 a.m., 10.0 p.m., and various other hours. It has been shown that when approaching or recovering from a moult the normal activity of an insect is profoundly disturbed, so that records obtained of an insect one day before or after a moult were not used in working out the results of this experiment, and in 4th and 5th instar insects, two days before and one day after a moult.

To compare the distribution of the activity shown by different individuals and by the same individual on different days, the amount occurring in each half of a record was expressed as a percentage of the total in that record.

A summary of the results is shown in Table VI, where the records are classified under the headings of those started at 10.0 a.m., those at 10.0 p.m., and those at other times. In each category an average is taken of the percentage of the total activity occurring in the second half of all the records available for the stadium concerned.

TABLE VI.

Stadium	Percentage of total activity occurring in 2nd half of records							
	Records started at 10.0 a.m.		Records started at 10.0 p.m.		Records started at other times		Total number of records	Average of all records
	Number of records	Average	Number of records	Average	Number of records	Average		
1	—	—	—	—	10	90	10	90
2	5	75	7	79	12	84	24	80
3	9	75	7	79	19	79	35	78
4	5	89	7	78	17	82	29	82
5	6	83	5	78	31	76	42	77
Adults up to 7 days old	10	75	9	71	20	74	39	73·5
Adults over 7 days old	—	—	—	—	108	57	108	57

In the adult stage it was found that insects up to seven days old behaved as regards the distribution of each day's activity in the same way as the nymphs, but that after seven days the percentage of the total daily activity which occurred in the second half of each record decreased irregularly until the activity was distributed nearly equally in both halves. Records of adults up to seven days old are therefore separated from those older than seven days and treated in the same way as the nymphs.

The figures obtained from these experiments show that there is a considerable variation in the proportion of activity in either half, but that no matter at what hour of the day the record is started, the greater part of the activity always occurs in the second half.

It can be said then that there is no diurnal periodicity in activity associated with any particular time of the day.

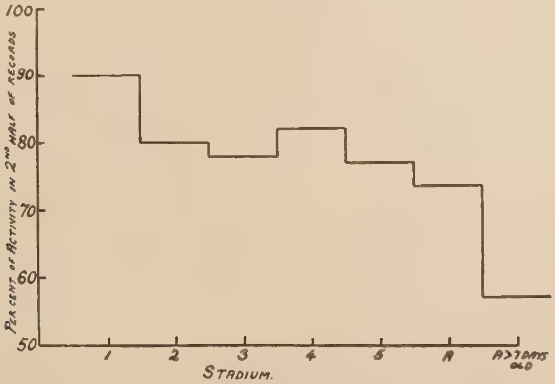


Fig. 6. Histogram showing the proportion of the total activity which occurs in the second half of records at different stages.

The figures in the last column of Table VI, which represent the average percentage of activity in the second half of all records for each stadium, show an irregular decrease from 90 per cent. in the first instar to 57 per cent. in the adults over 7 days old. The difference between these figures was tested statistically, and it was found that the difference between 90 per cent. for the first instar and 80 per cent. for the second was significant. The differences between the figures 80 per cent., 78 per cent., 82 per cent., 77 per cent. and 73·5 per cent. for the 2nd to 5th instars and adults up to seven days old were not significant, and the difference between any of those figures and the 57 per cent. for adults older than seven days was statistically significant. These figures are expressed graphically in fig. 6, and will be discussed later in the light of further experiments.

Relation between Activity and Hunger.

Having established that no diurnal periodicity exists in the insect, the unequal distribution of activity in each record requires explanation. The conditions of light and temperature were constant, but the relative humidity varied very considerably. In the first half of each record the relative humidity in the activity cages was high, owing to the presence of moist grass, which, however, dried out in the second half and left a relatively low R.H.

This assumption was tested by measuring the humidity in an activity cage at frequent intervals up to 24 hours. The appropriate amount of grass was cut and placed in the cage, together with a hygrometer. The cage was then closed and readings of the hygrometer were taken every half hour.

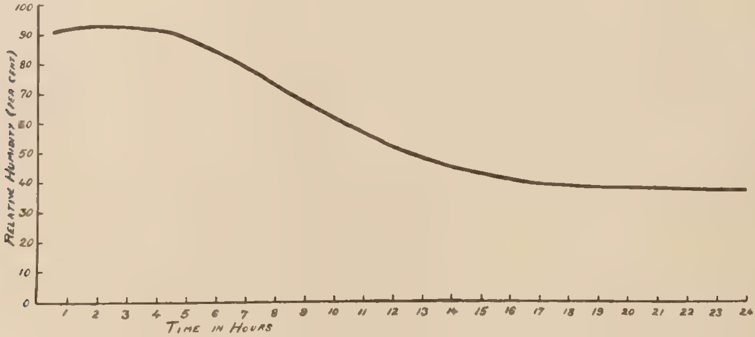


Fig. 7. Variation in relative humidity in an activity cage during 24 hours with fresh grass at the beginning.

The curve in fig. 7 was constructed from over 100 readings obtained in this manner. It shows the fluctuations in relative humidity inside an activity cage over 24 hours with fresh grass at the beginning. There is a high humidity for the first 6 hours, which falls off during the next 12 hours to a relatively low humidity in the last 6 hours.

Only cages used for the 5th instar and for the adult stage were used in the above determinations, since the other cages were too small to allow a hygrometer to be enclosed. It was assumed that the variation in humidity in these smaller cages was similar to that in the larger ones, as the amount of fresh grass was always roughly proportional to the size of the cage.

The relative humidity, then, is one factor which varies during the course of a record. Another is the degree of hunger (and thirst) of the insect, since it has fresh food in the first half and none in the second. No other factor varies in this way, so that it can be concluded that one or the other, or a combination of the two, is responsible for the uneven distribution of activity. It was decided to investigate this question further, and the problem was approached by performing three experiments.

TABLE VII.

Distribution of Activity over 48 *Hours.*

Conditions :—

1st 12 hours : food, high humidity.
2nd 12 hours : no food, low humidity.
3rd 12 hours : no food, low humidity.
4th 12 hours : no food, low humidity.

Instar	Record no.	Time started	Insect no.	Sex	Total activity	Percentage of total activity occurring in			
						1st 12 hrs.	2nd 12 hrs.	3rd 12 hrs.	4th 12 hrs.
2	231 232	12 day	220		240	2	18	44	36
	233 234	,,	,,		102	2	10	43	46
	A196 A198	,,	265		902	3	7	34	56
					Average	2	12	40	46
3	235 236	12 day	210	F	696	4	16	44	36
	237 238	,,	,,	,,	1044	1	9	28	62
	273 274	1 p.m.	265		363	10	24	26	40
					Average	15	16	33	46
4	196 197	12 day	193	M	1067	3	12	13	71
	285 286	1 p.m.	250	F	1038	0	4	29	67
	289 290	1 p.m.	253	F	3412	1	14	41	44
					Average	1	10	28	61
5	200 201	12 day	185	M	1992	2	17	41	40
	291 292	1 p.m.	256	M	809	1	20	57	22
	A216 A217	12 day	248	M	2335	6	22	36	36
					Average	3	20	44	33
Adult	A231 A232	12.30 p.m.	260	M	188	12	24	34	30
	301 302	1.0 p.m.	255	M	460	1	12	38	49
	303 304	12.30 p.m.	248	M	444	13	11	44	32
					Average	9	16	38	37
			Average for all records ...			4	15	37	44

In the first, records were taken of insects of all stages except 1st instars and old adults. An insect was given food in the usual quantity which lasted for 12 hours. After the first record of 24 hours the dry grass was removed from the cage and the insect replaced, this time without any food and the activity recorded for a further 24 hours.

Each 48-hour record therefore consisted of two 24-hour records, in the first of which food was present and the humidity consequently high for the first half, and food absent and the humidity low for the second half ; in the second record food was absent and the humidity low the whole time.

The results of this experiment are shown in Table VII. Three 48-hour records were taken of each instar, and again the percentage of total activity occurring in each 12-hour period was made the basis of comparison. An average was taken for each instar, but probably the only reliable figures are those given in the average for all records.

The figures all agree in showing very much more activity in the second 24 hours than the first. All except one adult agree in showing an increase in the activity in the second 12 hours over that in the first and a further increase in the third over the second. The majority show a still further increase in the fourth 12 hours over the third.

The effect of prolonged starvation was investigated in two adult insects. The activity of each was recorded continuously in 24-hour periods with food at the beginning of the first record only. In both insects the activity increased up to the fourth 12-hour period and then rapidly decreased until the insects were found dead after the fourth 24-hour record. One insect showed no activity in the last 12-hour period, the other showed a little. It seems, then, that the effect of starvation in decreasing the amount of available energy begins between 36 and 48 hours after the last feed.

The conclusion to be drawn from the results shown in Table VII is that the factors at work become increasingly more effective, certainly up to 36 and usually up to 48 hours.

The second experiment in this series was performed like the first except that after the first 24-hour record a fresh supply of grass was put into the cage and covered over with a perforated zinc screen which prevented the insect from eating it, but which allowed it to dry out in the normal manner.

Each 48-hour record in this experiment consisted again of two 24-hour records ; in the first, the first 12 hours were with food and high humidity, the second 12 without food and low humidity. In the second 24-hour record the first 12 hours were with high humidity but without food, and the last 12 without food and with low humidity.

The results of this experiment are shown in Table VIII. The figures here are similar in essentials to those obtained in the last experiment. There is in every record a much larger amount of activity in the second 24 hours than in the first. The figures also agree in showing an increase in activity from the first to the third 12-hour period and in half the records to the fourth. The average for all records in this experiment actually shows a decrease in the amount of activity occurring in the last 12-hour period from that in the third 12-hour period. The difference is not, however, statistically significant.

The crucial point in comparing the results of this experiment and the last is the difference shown in each between the percentage activity occurring in the second and third 12-hour periods, since the conditions of humidity were the same over these two periods in the first experiment and varied in the second. The difference is an increase of 22 per cent. in the first experiment and 19 per cent. in the second, a correspondence close enough to suggest that a variation in humidity has little or no effect on the amount of activity.

TABLE VIII.

Distribution of Activity over 48 *Hours*.

Conditions :—

1st 12 hours : food, high humidity.
2nd 12 hours : no food, low humidity.
3rd 12 hours : no food, high humidity.
4th 12 hours : no food, low humidity.

Instar	Record no.	Time started	Insect no.	Sex	Total activity	Percentage of total activity occurring in			
						1st 12 hrs.	2nd 12 hrs.	3rd 12 hrs.	4th 12 hrs.
2	A199 A200	12	250	F	347	2	24	62	12
	A235 A236	12.30	288		390	5	25	41	29
	A271 A272	12.30	305		1420	2	26	40	32
	307 308	1.0	286		234	17	20	18	45
					Average	7	24	40	29
3	239 240	12	210	F	891	6	31	34	28
	241 242	12	210	F	1093	16	20	46	18
	299 300	12.30	272	M	846	16	31	33	20
					Average	13	27	38	22
4	287 288	1 p.m.	250	F	2640	9	23	34	34
	A229 A230	12.30	273	M	1020	5	14	56	25
	A233 A234	1 p.m.	277	M	840	1	9	41	49
					Average	5	15	44	36
5	A175 A176	12	212	F	2396	2	7	34	57
	205 206	12.30	193	M	2158	3	9	32	56
	295 296	12.30	252	F	1310	5	23	39	33
					Average	3	13	35	49
Adult	A239 A240	12.30	243	F	462	3	22	35	40
	319 320	12.30	273	M	243	3	10	41	46
	A257 A258	11.0 a.m.	277	M	185	3	22	36	39
					Average	3	18	37	42
			Average of all records			6	20	39	35

The third experiment of this series consisted of taking records of activity under conditions of constant humidity but with variations in the degree of hunger. A special activity cage was constructed for this purpose in which the humidity could be kept constant. A diagrammatic section through this cage is shown in fig. 8. It consisted of an airtight aluminium box (A), of the same size as an ordinary activity cage, 9 ins. by 3 ins. by 2 ins. The lid was made of a framework of aluminium (L) into which was fixed a piece of celastoid (C). A thin strip of plasticene was pressed all round the edge of the celastoid for added security. The lid was made to fit the box closely, and when the box was in use the contact (E) between the edge of the lid and the box was sealed with vaseline.

A tray, $\frac{5}{8}$in. deep, made of tin and divided into eight separate compartments, was placed in the bottom of the box and a saturated solution (with excess of the solid phase) of a salt giving the required relative humidity was introduced into each compartment. A piece of perforated zinc cut to fit the cage closely was then put on top of the tray, and this formed a floor for the insect to walk on.

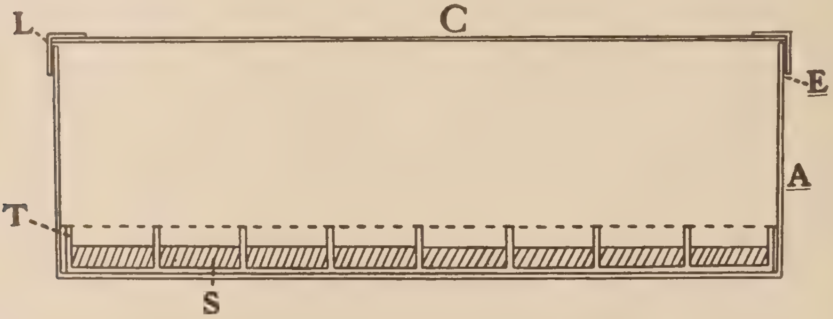


Fig. 8. Humidity Cage—A, Aluminium Cage; C, Celluloid Top; E, Contact between Lid and Box; L, Framework of Lid; S, Saturated salt solution; T, Tray.

The weight of this cage was inevitably much greater than that of any celastoid cage, so that an extra strong beam had to be used. Increased sensitivity was obtained by attaching the cage above the beam instead of below it, as in fig. 1, and using a different counter-balancing weight which could be moved along the top of the beam.

For controlling the humidity in the cage it was decided to use a solution of sodium chlorate; this was found to give a relative humidity of 79 per cent. at 27°C. and remained constant in the humidity cage for at least 48 hours, which was the longest observation made.

Records of activity over 24-hour periods were then taken, using this cage with adult insects up to seven days old; the nymphs were found to be too light for accurate determination.

The results of this experiment are shown in Table IX. The records are divided into two sections, (*a*) those in which an insect had food at the beginning, and (*b*) those in which no food was given. Since there was a constant relative humidity of 79 per cent. in the cage, it cannot be said that the grass dried out at the same rate as in the previous experiments, but it was found that even insects starved for periods up to 12 hours would not eat grass that had been exposed for 24 hours to this humidity. It can therefore be said that the grass became unpalatable some time during the second 12 hours, and we have the following conditions: (*a*) Records in which food was given; high humidity throughout the 24 hours, food present in the first 12 and absent for some part of the second 12 ; (*b*) records in which no food was given ; high relative humidity throughout, no food throughout, and the insects therefore increasingly hungry.

TABLE IX.

Distribution of Activity over 24 Hours ; all Adults up to 7 Days old.

(*a*) 1st 12 hours : high humidity, food present.
2nd 12 hours : high humidity, food absent for part of time.

Record number	Insect number	Time started	Days after moult	R.H. per cent.	Total activity	Percentage occurring in	
						1st half	2nd half
A260	279	11.40 a.m.	2	79	11	9	91
A261	279	11.40 a.m.	3	79	125	11	89
A262	279	11.40 a.m.	4	79	134	33	67
A264	279	12.0 day	5	79	40	12	88
340	295	12.0 day	1	79	21	5	95
342	295	1.0 p.m.	3	79	18	6	94
A282	296	3.0 p.m.	4	79	12	25	75
			Average of	all records	... ...	17	83

(*b*) High humidity throughout, no food throughout.

Record number	Insect number	Time started	Days after moult	R.H. per cent.	Total activity	Percentage occurring in	
						1st half	2nd half
A263	279	11.35 a.m.	5	79	127	57	43
341	295	12.0 day	2	79	167	32	68
343	295	1.0 p.m.	4	79	274	45	55
345	295	1.0 p.m.	6	79	408	44	56
A281	296	3.0 p.m.	3	79	45	55	45
A283	296	3.0 p.m.	5	79	74	65	35
			Average of	all records	... ...	50	50

The figures for series (*a*) all agree in showing a higher percentage of activity in the second half than in the first, the difference between the average figures being 66 per cent. Here, then, in spite of a constant high humidity we find there is still a greater proportion of the total activity in the second half of all records than in the first. As the degree of hunger was the only factor that varied, it is highly probable that this is the important factor in controlling activity.

The figures in series (*b*) vary rather widely. There are, unfortunately, not enough records to allow of any definite conclusion being drawn. The total amount of activity in each record is on the whole higher than the total amount in records where food was present ; also, the average figures show an equal amount of activity occurring in each half. The insects used in this experiment had been used during the 24 hours prior to determination either for a record in series (*a*), in which case they would have been without food for approximately 12 hours, or else they had been kept apart from food for 16 hours. It was therefore to be expected that there would be no large increase in activity in the second half of these records as prolonged starvation would begin to decrease the amount of available energy.

Summarising the results of these three experiments, it has been found that if an insect is allowed food for 12 hours and then starved, the conditions of humidity being high for 12 hours and then low, the activity shown by the insect increases up to 36 hours after the food has dried out and the humidity fallen. If the humidity is raised after 24 hours have passed and falls again after a further 12 hours, the other conditions remaining the same, the distribution of activity is not affected.

Under conditions of constant high humidity for 24 hours with food present for at least the first 12 and absent for something less than the last 12, the amount of activity shown by the insect is greater in the second 12 hours than in the first. If under these conditions of constant high humidity an insect previously starved for at least 12 hours is given no food, the activity is high for 24 hours.

The conclusion to be drawn from these results is that an increase in the degree of hunger experienced by an insect produces an increase in activity up to about 36 hours after the last opportunity of feeding, but that a variation of relative humidity between 95 per cent. and 35 per cent. has little or no effect.

Periodicity in Activity.

(*a*) *Diurnal, induced by light conditioning.*

Although locusts kept from the time of hatching under constant conditions show no diurnal periodicity, it was not known whether such a periodicity could be induced in the insects if kept under conditions of normal alternation of night and day.

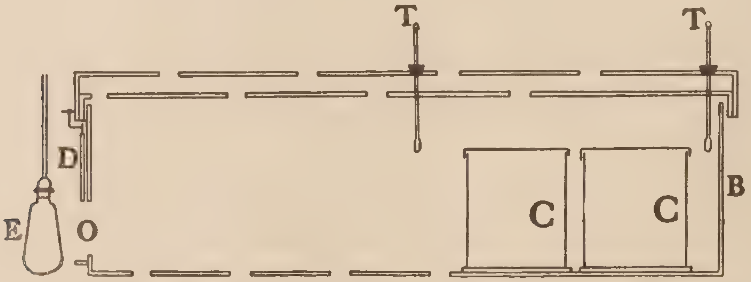


Fig. 9. Light conditioning Box. B. Box ; C. Cage ; D. Sliding Door ; E. Light ; O. Opening ; T. Thermometer.

An apparatus was constructed in which hoppers could be kept from the time of hatching under conditions of alternating 12-hour periods of light and dark. A diagrammatic section through this apparatus is shown in fig. 9. It consists of a large cardboard box (B), 4ft. long by 14 ins. high by 12 ins. wide, in which the temperature could be kept constant but light conditions changed.

Two hoppers were conditioned in this way, their living cages (C) were placed at one end of the box and light from a 40-watt vacuum bulb (E) hung outside the box was admitted through an opening (O), 4 ins. square and exactly opposite the bulb.

It was decided that from 12.0 mid-day to 12.0 midnight should be dark and from 12.0 night to 12.0 noon light. This allowed the insects to be fed during the light period before 12.0 in the morning. At mid-day the light was switched out and the opening covered by a sliding door (D). The box was then light-proof and the insects remained in darkness until midnight, when the light was automatically switched on and the sliding door automatically pulled up to allow the light to enter the box.

The temperature inside the box was measured by two thermometers (T), one in the middle and one at the end farthest from the source of light. The box was used in the C.T. room so that an even temperature of 27°C. was assured when the light was out. The lid was made double and holes were bored through it in such a way that air could flow out but no light could enter (fig. 9). Holes were also made in the bottom of the box, which was raised about 2 ins. from the ground, to allow air to enter. In spite of these precautions, when the light was on the temperature was found to be raised about 1°C. in the middle of the cage and 0·5°C. at the further end, and this small fluctuation was neglected.

The insects were kept under these conditions from the time of hatching, and records of their activity were taken in the adult stage at intervals from the 14th day after emergence onwards. The records in the first series were started at 12.0 mid-day, an ordinary adult activity cage was used, and 1 gm. of fresh grass was given.

The light conditions during each 24-hour record were the same as those to which the insect had been previously accustomed, that is, the first 12 hours were in darkness and the second 12 in light. At midnight the light was automatically switched on and a black cloth cover removed from the light opening directly over the activity cage.

The results of this series of records are given in Table X. Both insects showed far more activity in the 12 light hours than in the 12 dark, but the difference was such that it could possibly be accounted for by the absence of food in the second half, although, as has been shown above, the distribution of the activity of adults

TABLE X.

Periodicity induced by alternating 12-hour Periods of Light and Dark ; all Adult Insects.

Records started at 12.0 mid-day.

1st 12 hours dark ; 2nd 12 hours light.

Record no.	Insect no.	Sex	Days after after moult	Total activity	Percentage of total activity occurring in	
					1st half	2nd half
313	268	M	14	88	19	81
314	,,	,,	15	131	18	82
315	,,	,,	16	21	5	95
316	,,	,,	17	42	9	91
321	271	F	14	149	29	71
322	,,	,,	15	150	31	69
324	268	M	24	38	0	100
532	,,	,,	37	34	0	100

older than seven days is normally very nearly equal in both halves of a 24-hour record.

It is interesting to note that the last two of this series of records, taken when the insects had been adult for 24 and 37 days respectively, show no activity at all in the second half.

When an insect was not being used experimentally it was replaced in the light conditioning box and treated as before.

A second series of records was taken, starting at 12 midnight. In these records the first 12 hours were light and the second 12 dark. One gram of grass was given at the beginning of each record, so that in this series the 12-hour light period corresponded with the presence of food and the 12-hour dark period was without food.

The results, given in Table XI, show very nearly all the activity occurring in the light hours. In spite of the fact that there was no fresh food in the second half, practically no activity is shown. These results show clearly that a 12-hour alternation of light and dark has a profound effect on the diurnal distribution of activity. The insects, when the second series of records was taken, were older than they were in the first, which would suggest that the effect of this light conditioning becomes more marked the longer the insects are subjected to it.

TABLE XI.

All adult Insects.

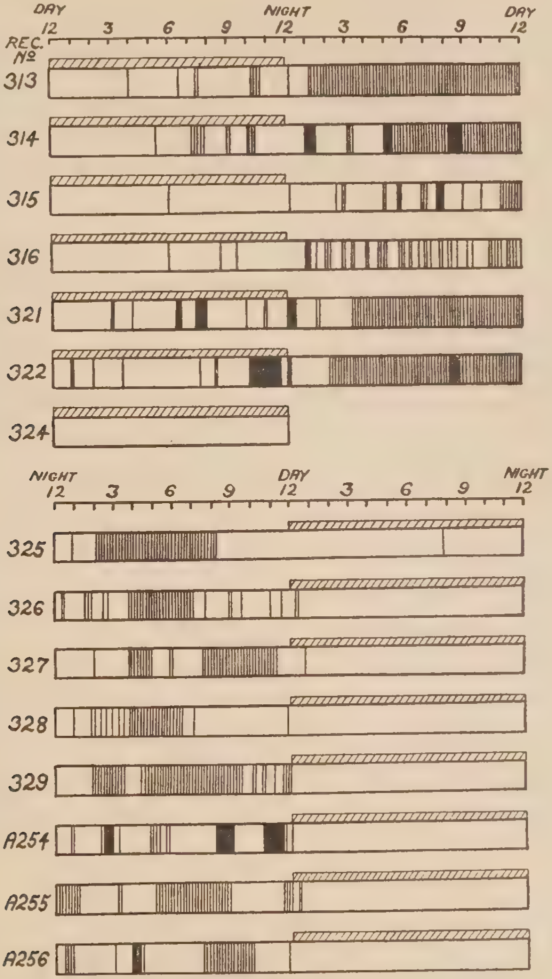
Records started at 12.0 midnight.

1st 12 hours light ; 2nd 12 hours dark.

Record no.	Insect no.	Sex	Days after moult	Total activity	Percentage of total activity occurring in	
					1st half	2nd half
325	268	M	25	38	100	0
326	,,	,,	26	21	90	10
327	,,	,,	27	25	96	4
328	,,	,,	28	20	100	0
329	,,	,,	29	31	100	0
A254	271	F	20	43	100	0
A255	,,	,,	21	47	96	4
S256	,,	,,	22	30	100	0

The detailed distribution of activity can be appreciated by referring to fig. 10 where each record is represented schematically, using the same method as described above. A striped bar above a diagram indicates that that part of the record was taken in darkness.

In order to ascertain whether this periodicity would persist under constant conditions, a third series of records was taken, this time in constant darkness. The records were started at 12 mid-day and the results obtained are given in Table XII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A254
A255
A256

Fig. 10. Schematic representation of records of light-conditioned insects. Striped bar above diagram indicates period of darkness. (See Tables 10 and 11.)

TABLE XII.

All adult Insects ; records in continuous Darkness, started at 12.0 *Noon.*

Record no.	Insect no.	Sex	Days after moult	Total activity	Percentage of total activity occurring in	
					1st half	2nd half
333	268	M	38	45	2	98
334	,,	,,	39	32	6	94
335	,,	,,	40	21	5	95
336	,,	,,	41	26	8	92
337	,,	,,	42	33	3	97
338	,,	,,	43	26	19	81
339	,,	,,	44	25	32	68
A274	,,	,,	48	33	39	61
A277	,,	,,	51	93	45	55

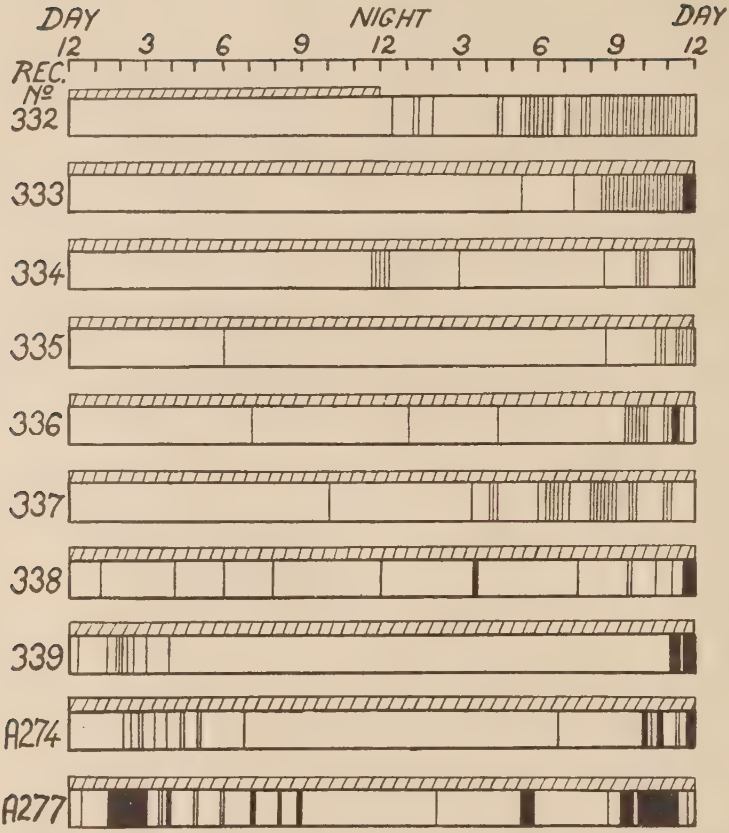

Fig. 11. Schematic representation of light-conditioned insects. Records (except No. 332) in continuous darkness. See Table XII.

and fig. 11. Only the male insect could be used in this series as the female died. The records were taken on the 38th to 44th days after emergence and on the 48th and 51st days. The figures in Table XII, when considered together with the diagrams in fig. 10. show that the periodicity does persist for a few days, after which the activity slowly becomes distributed more equally.

(*b*) *Intrinsic periodicity.*

We come now to consider the possible existence in the locust of any short period rhythms in activity. During the course of the experiments described above, it was noticed that a number of records did show a very definite alternation between periods of activity and inactivity, and that the periods of activity were often separated by roughly equal periods of rest.

Fig. 16, B, is a reproduction of one of the records of an adult female in which periodicity is shown, the arrows in the upper margin indicate "periods of high activity" which are used as indications of the rhythm. Fig. 12 shows schematically a selection of records which were considered to show indications of periodicity and were used in the following investigation.

It was clear that many records showed no sign of periodicity and as the inclusion of these in an examination for periodicity would obscure its possible presence elsewhere it was decided to examine only those records in which indications of periodicity were apparent. It was also noticed that such " periodic " records showed relatively few short rest periods, that is, rest periods of less than 30 minutes, as compared with the number shown in other records. This was chosen as an arbitrary method of separating out those records which were to be examined for periodicity.

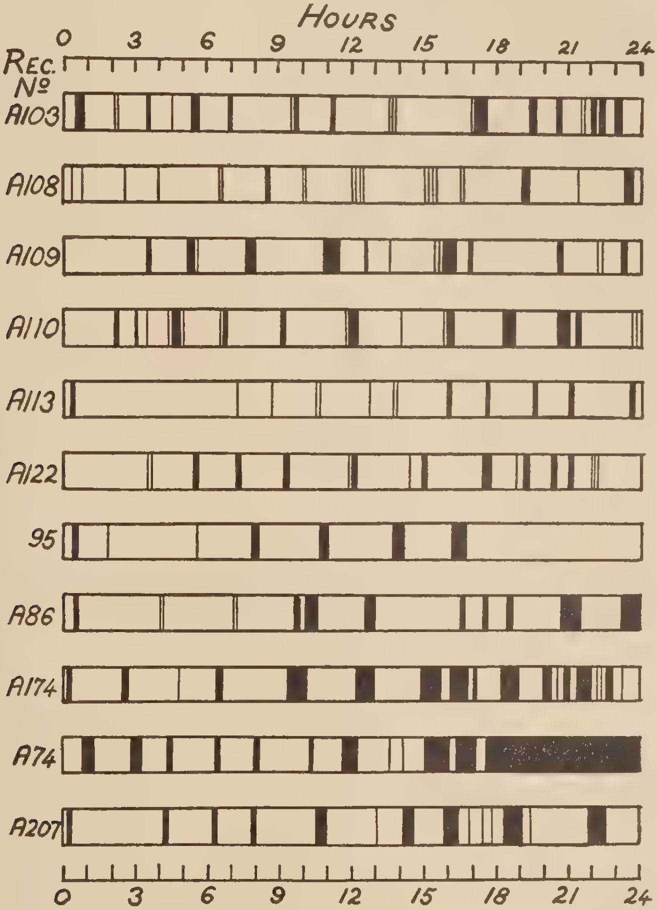

Fig. 12. Schematic representation of records showing periodicity.

A 103–A 122. Adult female No. 163.
95–A 174. 5th Instar insects Nos. 51, 163 and 212.
A 74 and A 207. 4th Instar insects Nos. 163 and 248.

A frequency curve was plotted for all records, whether indications of periodicity were apparent or not, to show the number of rest periods of less than half an hour which appeared in each record. The curve was found to be bimodal, the records in which indications of periodicity were present showed up to 8 of such short rest periods with a mode at 4, and the other records showed from 9 to 35, with a mode at 14. All records which showed 8 or fewer rest periods of less than half an hour were then examined for periodicity; 69 records were thus selected for further examination, of which 38 were of adult, 18 of 5th instar and 13 of 4th instar insects. No 2nd or 3rd instar records showed any indication of periodicity.

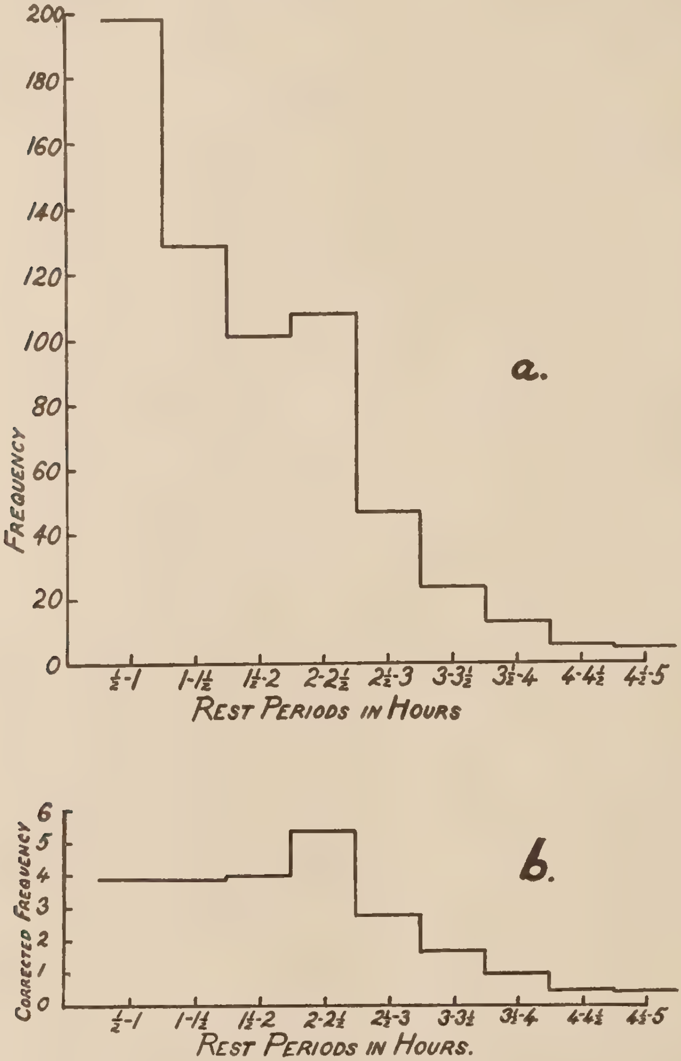

Fig. 13. *a*, Frequency of rest periods of different lengths. All records examined for periodicity. *b*, "Corrected" frequency of rest periods. (See Table XIII).

The examination of these arbitrarily selected records was then made by two methods. Firstly, the lengths of the rest periods in all records were measured to the nearest half hour, the length of a rest period for this purpose being determined by the length of a horizontal line on the record and being deemed to continue until interrupted by at least one stroke on the record, that is, until the insect had travelled one length of the activity cage. Rest periods of less than half an hour were neglected.

The rest periods in all the records examined were then classified under the headings : ½ hour–1 hour, 1 hour–1½ hours, and so on up to 4½–5 hours. The results for each stage and the total for all stages examined are given in Table XIII and in fig. 13*a*. The histogram resembles half of a symmetrical curve (except for an excess of 2–2½ hour rest periods) such as might be expected if the frequency of a rest period depended on its length (*i.e.*, the shorter the period of rest the more likely its occurrence). If this were really the case, quantities obtained by multiplying the frequency of each rest period by the length of period should all be equal. In Table XIII this multiplication has been performed and the resulting quantities divided by 100 and expressed as "corrected frequencies." In the graphical representation of these quantities, fig. 13 *b*, the excess of 2–2½ hour rest periods is even more apparent than in fig. 12 *a*.

TABLE XIII.

	Length of rest periods in hours.								
Stadium ...	½–1	1–1½	1½–2	2–2½	2½–3	3–3½	3½–4	4–4½	4½–5
4th Instar	30	20	16	18	8	6	4	1	1
5th Instar	38	20	24	21	12	7	2	2	2
Adult ...	130	89	61	69	27	11	7	3	2
Total ...	198	129	101	108	47	24	13	6	5
Corrected frequency ÷ 100	3·9	3·9	4·0	5·4	2·8	1·7	1·0	·5	·5

TABLE XIV.

	Time between periods of high activity in hours.								
Stadium ...	½–1	1–1½	1½–2	2–2½	2½–3	3–3½	3½–4	4–4½	4½–5
4th Instar	4	7	14	16	6	4	4	2	1
5th Instar	6	10	15	14	23	13	11	3	1
Adult ...	32	45	55	68	35	16	6	1	3
Total ...	42	62	84	98	64	33	21	6	5

The second method of procedure was to measure the time between the middle of one period of high activity and the middle of the next. For this purpose a "period of high activity" was defined as any period of activity of at least two full strokes separated from the next period by at least half an hour. The results of this method of treatment are given in Table XIV, and the total frequency for all stages studied is shown graphically in fig. 14. This histogram shows clearly the tendency for more 2–2½ hour intervals between periods of high activity to occur than any other intervals. As the meaning of the curve can be readily appreciated when constructed from the original figures the frequencies obtained by this method need no correction.

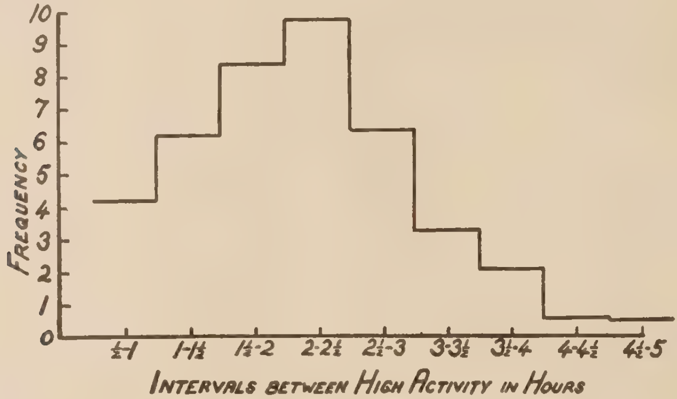

Fig. 14. Frequency of intervals between periods of high activity. (See Table XIV.)

The explanation of this difference is that by the method of measuring the lengths of all rest periods a large number of small values are obtained, whereas an interval between two periods of high activity may include more than one short rest period. A reference to fig. 16, B, will make this clear.

The mode of the curves obtained by both methods is the same—between 2 and 2½ hours. It can therefore be said that there is a tendency for periods of activity to alternate with periods of rest and that the periods of activity recur at intervals of 2–2½ hours more often than at any other interval.

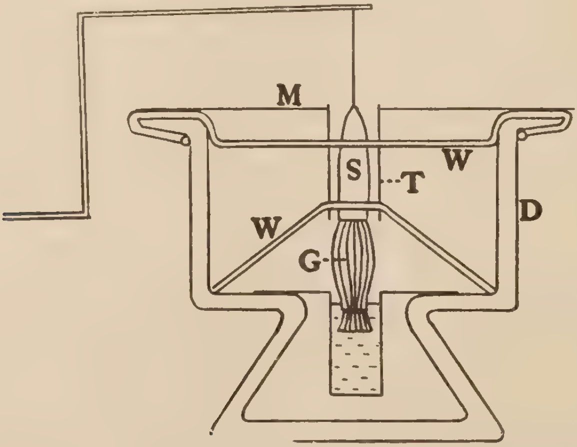

Fig. 15. Trophograph apparatus. D, Desiccator; G, Grass; M, Muslin cover; S, Tinfoil cap; T, Glass Tube; W, Wire supports.

It would appear to be possible that the irregular 2–2½ hour periodicity found in the locust is associated with a form of hunger rhythm. No such rhythm has been demonstrated in the locust, or, to my knowledge, in any other insect.

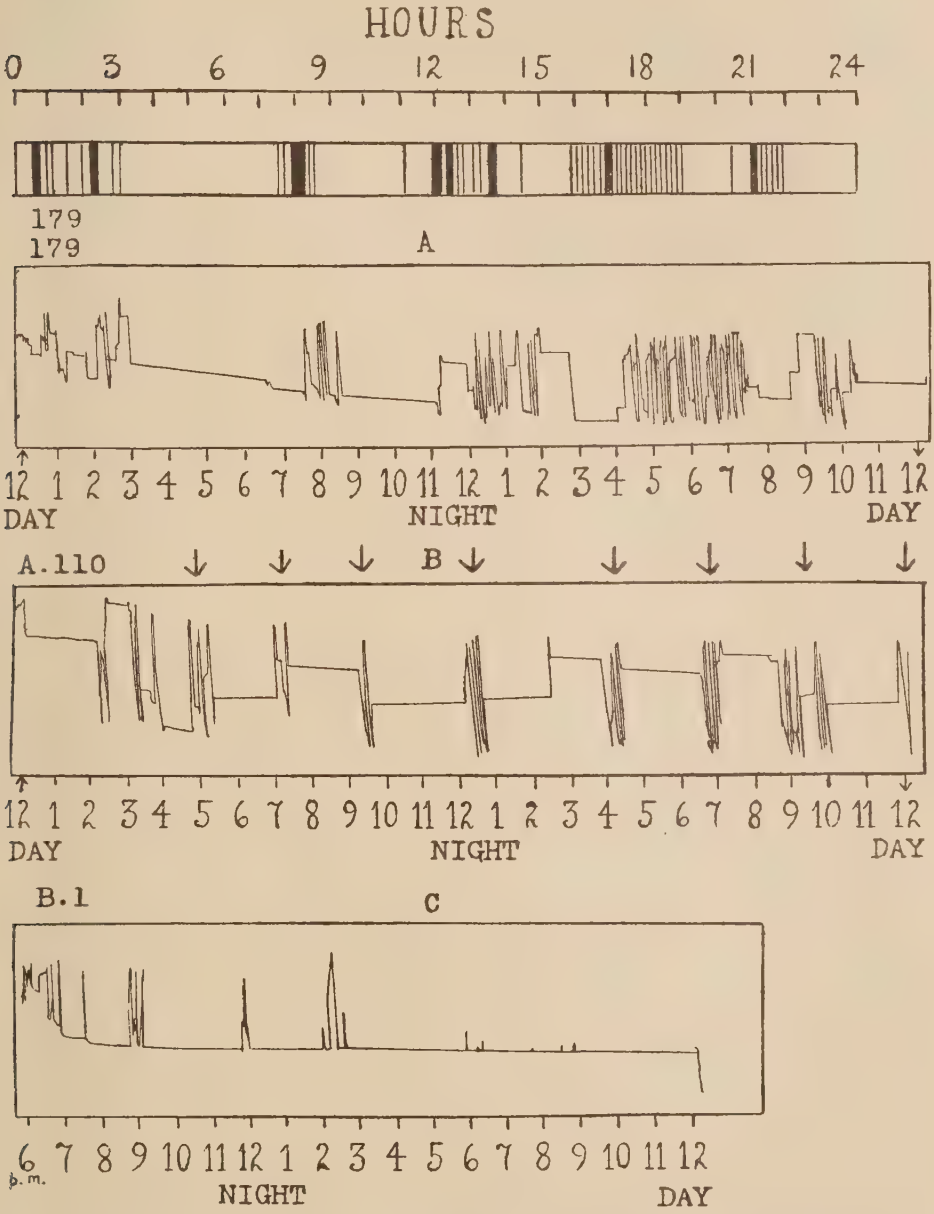

Fig. 16. A, Record No. 179, and schematic representation; adult male insect No. 114, 48th day after emergence. B, Record A.110; adult female No. 163, 17th day after emergence, showing periodicity; arrows in upper margin indicate periods of high activity. C, Trophograph record B.1; adult male insect.

In order to test this suggestion, several attempts were made at constructing a "trophograph" apparatus to record when an insect fed. Fig. 15 is a diagram of such an apparatus. It consists of a desiccator (D) covered in by a piece of muslin (M) held taut by a rubber band. This forms an activity and a feeding cage, though it is only feeding which can be recorded. Through a hole in the muslin a glass tube (T) projects inwards and is held in place by two supports of stout copper wire W).) Vertically below this tube in the well of the desiccator is another glass tube nearly filled with water and held by a sheet of thin metal which rests upon the floor of the upper compartment.

The food consists of a number of blades of grass (G) held tightly together by a strand of thin wire at one end and enclosed in a tin-foil cap (S) at the other. This is attached by a piece of cotton to one arm of an actograph beam and is allowed to hang in the cage with the free ends of the blades of grass in water. The position of the upper glass tube is so adjusted that the space between it and the floor of the cage is enough to allow the insect to feed on the grass but not to crawl on to it. As the insect feeds it pulls on the grass, and this is recorded by the writing point as a stroke on the smoked paper.

Several records were taken, using variations of this apparatus; they were not very successful owing to the imperfections of the apparatus. Fig. 16, C, is a reproduction of one of the records obtained. It does show indications of a periodicity in feeding, the time between periods being of the same order between periods of activity.

No definite conclusion can be drawn from an examination of these records, as too few reliable ones have been obtained to make a statistical treatment possible. Nevertheless, the records do suggest the possibility of a periodicity in feeding and show the question to be well worth further investigation.

Discussion.

In the present work we have been concerned chiefly with fluctuations in the amount of locomotor activity under constant conditions. The experimental conditions used were by no means optimum or natural, so that the results obtained can only be said to be true for the conditions which obtained at the time. It is reasonable to assume that a change in these conditions, for instance, an increase in the temperature, would alter the level of activity, but that the amount would still fluctuate about the new level. Whether it would fluctuate in a similar manner is not certain; a similar set of experiments under conditions as nearly natural as possible would be of great value in answering this and other questions.

It is unfortunate that the conditions of food could not be controlled during each 24-hour period more satisfactorily than they were. The locust, from this point of view, is an unsuitable animal for actograph experiments, since it needs a constant supply of moist grass. An absence of fresh food has been shown to have the effect of increasing the amount of locomotor activity and the effect is not the same in all stages of the insect. This is shown clearly in fig. 6. The proportion of the total activity which occurs in the second half of each record is as much as 90 per cent. in the 1st instar and falls to only 57 per cent. in adults over seven days old. The irregularity of the curve may be due to an insufficient number of records; but that the effect varies from one stage to another is certain.

In the light of this conclusion Key's method of conditioning his insects by keeping each individual without food for four hours before determination, is not entirely satisfactory, since the extra amount of activity induced by this amount of starvation would not be the same for individuals of different stages.

No work has been done on the effect of starvation on the activity of other insects, so that no comparison can be made, but that hunger can profoundly affect the physiology of an insect is shown by Bodenheimer & Schenkin (1928). They found that the normally preferred temperature of *Tribolium confusum* was 26°C., but hungry individuals preferred 19°C., only moving after a long time to the original preferendum.

The effect of humidity on the activity of the locust has been found in the present work to be very slight or absent. The results obtained by Key are not contrary to this conclusion, and those of Miller (1929), who found changes of humidity to have no effect on the rate of locomotion of fly larvae, are in agreement with it. The present results for the locust refer only to variations in relative humidity from 35 per cent. to 95 per cent. and the effect over 24 hours. It is not known whether a longer exposure to certain humidities, or to humidities outside the range used in the present work, would have a greater effect.

It is to be regretted that a further experiment could not have been added to those described in section 3 in which the distribution of activity would have been measured under conditions of a constant supply of food, but with varying humidity. The difficulty in performing such an experiment lies in the fact that the insects need moist food, and even if it were possible to keep the food fresh for 24 hours it would be impossible to lower the relative humidity without drying out the food.

An important point not covered by the present investigations is the separation of the factors hunger and thirst. However, as thirst is inseparable from desiccation, the present results, by showing that the relative humidity has no demonstrable effect on the amount of activity, suggests that the effect of thirst is small and that the increase in activity is brought about largely by hunger.

It has been shown in the present work that locusts reared in alternating periods of light and dark are active during the light period and show almost complete rest during the dark period. The periodicity is retained only for a few days in continuous darkness, but no definite conclusion could be drawn as regards the effect of darkness on the level of activity.

Diurnal periodicities under alternating light and dark conditions have been demonstrated for several other Orthoptera by Lutz (1932). *Gryllus domesticus* showed a chief period of activity from 7.0 p.m. to midnight each day, with a maximum at 9.0 p.m. This periodicity was retained in continuous darkness, though the author does not say for how long. *G. assimilis* retained a diurnal rhythm for at least two weeks in constant darkness. The time of the active period could be changed by reversed conditions and the reversed periodicity retained in continuous darkness.

Whether the amount of activity is increased by constant light conditions appears to depend upon the normal habits of the animal concerned. Nocturnal animals show increased activity in continuous darkness. Park and Keller (1934) found the cockroach, *Parcoblatta*, to be continuously active in the dark until fatigue set in. Diurnal animals, on the other hand, show increased activity in continuous light, as was demonstrated by Szymanski for the canary. Meunier (1929), working on the cockchafer, *Melolontha melolontha*, L., was able to show a close relation between light intensity and swarming each day.

These results, together with the present work on the locust, lead to the conclusion that the effect of light conditions on the distribution of the activity of insects is very great but by no means deep-seated, since induced periodicity can be easily changed or eradicated by altering the light conditions.

Szymanski, as a result of his work on a large variety of animals, including the cockroach, probably *Blatella germanica*, came to the conclusion that the number of activity periods in a 24-hour cycle was constant for any one species ; further, that each species showed a definite amount of activity in a day and the amount under similar conditions was constant from day to day, but might vary at different stages of the animal's life. He also found that the higher the animal in the evolutionary scale the more constant were these periods and amounts. If these conclusions are correct, the very great variation in the amount of activity shown by the locust must be attributed to the relatively low position of the animal in the evolutionary scale, since neither the number of activity periods nor the amount of activity is constant from day to day.

Szymanski did not attach much importance to the effect of hunger on activity. He came to the conclusion that an activity peak is brought about by inner factors rather than by external ones or hunger, and that hunger cannot account for the occurrence and length of high activity periods.

The results of the present investigation show that the above conclusion cannot be applied to the locust studied, where hunger has a very profound effect upon the occurrence and duration of activity.

The importance of allowing for spontaneous variations when conducting any activity experiments is demonstrated by the results of the present work on the variation over different stages of the life of the insect. The unavoidable inclusion of a period of slight starvation in each 24-hour record renders the figures representing the amount of activity merely of relative value ; they do not represent the actual amount of activity which a locust could be expected to show if fresh food were always present. However, as the conditions were approximately the same for all individuals, the comparisons between various individuals and stages are valid.

The presence of a 2–2½ hour periodicity in the activity of the locust is of interest, as no such short periodicity has been observed in any other insect. It must be emphasised, however, that it is only present in a minority of records. This would suggest that it is very easily masked by other more powerful factors, in particular by factors which lead to a general increase in activity. What those factors are, and what is the cause of the periodicity, provide interesting questions.

It is possible that under conditions of temperature, light and humidity different from those used in the present experiments the periodicity would be brought out more clearly. On the other hand, the indefinite qualities may be due simply to the absence of adequate nervous mechanism.

As to the cause of the periodicity the preliminary experiments made with a trophograph apparatus suggest that it is associated with a hunger rhythm. The difficulty which occurs here is that as much variation and masking must be expected in a feeding periodicity, if present, as in the activity periodicity. It should be made sure, therefore, that an animal which is being tested for a feeding periodicity is showing at that time periodic activity. An ideal apparatus would be one in which both locomotor and feeding activity could be recorded simultaneously, otherwise even if a periodicity in feeding were demonstrated, the true relation between it and the periodic activity would still be doubtful.

Summary and Conclusions.

An actograph apparatus is described for recording in 24-hour periods, under controlled conditions, the activity of *Locusta migratoria migratorioides* (R. & F.) in terms of distance travelled.

Great variation was observed in the amount of activity shown by different individuals and the activity of any one individual is shown to vary considerably over each stadium, the highest level occurring about half-way between moults, and falling off towards the beginning and end of each stadium.

An insect is shown to be capable of very intense activity immediately before a moult if no convenient moulting place is found.

No significant difference is found between the activity of males and females, but the average distance travelled in a 24-hour period in the 4th and 5th stadia is shown to be greater than that in the 2nd or 3rd.

The daily activity of adults is shown to vary considerably from day to day, and the diurnal distribution of the activity of adults up to seven days old is shown to be similar to that of nymphs.

The unequal distribution of activity over each 24-hour period is shown to be due to absence of fresh food in the second half of each record, and the effect of this starvation is shown to vary according to the stage of development of the insect.

The effects of changes in relative humidity on the amount and distribution of activity are shown to be very slight or none.

A diurnal periodicity is shown to be induced in the insects when reared under alternating 12-hour periods of light and dark. The longer the conditioning lasts, the more clear-cut is the periodicity. In constant darkness the periodicity is retained for only a few days and gradually disappears.

A tendency for periods of high activity to recur every 2–2½ hours is demonstrated in certain records. In the other records, constituting actually the majority, it is suggested that the periodicity is masked or that the locust's nervous mechanism is inadequate to maintain it.

Preliminary experiments with a form of trophograph suggest that the 2–2½ hour periodicity may be associated with a hunger rhythm.

Acknowledgments.

The above work was carried out in the Department of Entomology of the Imperial College of Science and Technology while in receipt of a Charelick Salomon Scholarship.

I am indebted to Professor J. W. Munro, Dr. O. W. Richards and other members of the departmental staff for helpful criticism and advice. Also to Dr. K. H. L. Key for many useful suggestions, and to Dr. A. G. Hamilton of the Imperial Institute of Entomology for providing me with locusts and grass.

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NOTES ON THE DISTRIBUTION AND BREEDING-PLACES OF MOSQUITOS IN NORTHERN ABYSSINIA. (1)

By C. E. Bevan, M.A., B.Ch.(Cantab.), D.T.M. & H.

(Plate IX.)

Little is still known about the distribution of mosquitos in Abyssinia. The first record appears to be that of Theobald (1904) who described specimens collected by Balfour along the banks of the Baro and Pibor Rivers, which flow from Western Abyssinia into the Sobat, a tributary of the White Nile. Scott (1927) reported 13 species which he collected from Central Abyssinia, and he refers to two other species previously found by the Mission to Lake Tana (1925).

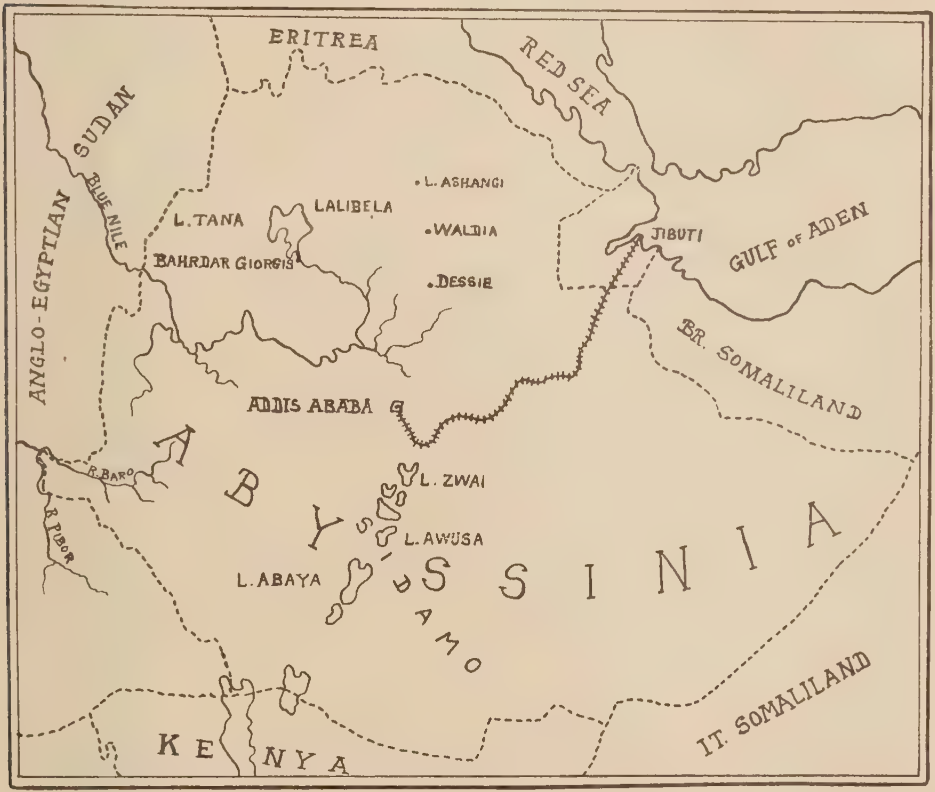
ERITREA
RED SEA
SUDAN
ANGLO-EGYPTIAN
BLUE NILE
L. TANA
LALIBELA
L. ASHANGI
WALDIA
DESSIE
BAHRDAR GIORGIS
JIBUTI
GULF OF ADEN
BR. SOMALILAND
ADDIS ABABA
R. BARO
R. PIBOR
L. ZWAI
L. AWUSA
L. ABAYA
SIDAMO
ABYSSINIA
IT. SOMALILAND
KENYA

Fig. 1.

The mosquitos recorded here were collected in collaboration with Dr. A. C. W. Barkhuus while we were serving with the British Red Cross Ambulance Service in Ethiopia from December 1935 to March 1936, during the Italo-Abyssinian War. Dr. Barkhuus should have been joint author, but he unfortunately fell ill at Waldia and is still ill in Denmark. The Ambulance was on the move for a great part of the time, and to avoid delay when travelling, tents were not usually pitched at night. All transport was by lorries over the most difficult roads imaginable. Owing to these conditions it was impossible to collect adult mosquitos or rear them from larvae when moving from one standing camp to another. The records are therefore limited to those places where the Ambulance remained long enough to enable mosquitos to be bred from larvae. Standing camps, where possible, were pitched away from obvious mosquito breeding-places, and it is partly for this reason that so few adults were found in the camps.

Method of rearing Mosquitos.

The majority of specimens obtained were bred from larvae or pupae. The chief difficulty experienced was the almost complete lack of entomological equipment. The entire apparatus consisted of a tin cup, an eye pipette, empty match boxes and cigarette tins, the remains of an old mosquito net and two small killing bottles. The rearing, killing and recording of the mosquitos obtained from the various breeding-places was performed by the writer in his 40 lb. living tent. Larvae or pupae caught in the dipping cup were transferred with an adequate quantity of water to cigarette tins ; a separate tin being used for each breeding-place. After labelling and replacing the lids the tins were brought back to camp, where they were opened and covered with pieces of mosquito netting. An empty matchbox, lined with a piece of tissue paper, was placed on the top of each tin and labelled with the same number as the tin below it. The numbered boxes helped to keep the netting in position, so preventing the escape of any adult mosquitos, while confusion between the different breeding-places was avoided. Each tin was inspected daily for adult mosquitos. After removing the matchbox, the piece of netting was raised up in the shape of a dome and the mosquitos were easily driven into this space by tapping the sides of the tin. The netting was then gathered in and removed while a fresh piece of material was slid over the top of the tin to prevent the escape of mosquitos that might remain. A killing bottle was inserted into the bag of netting and placed over the mosquitos one by one. The dead insects were then transferred to the appropriate matchbox. Each tin was treated in this way, and all mosquitos from one breeding-place were killed and packed away before the manoeuvres were repeated with the next tin. When rearing from one breeding-place was completed the matchbox was stored in an airtight tin. All specimens were sent to the Imperial Institute of Entomology and have been identified by Dr. F. W. Edwards.

The Ambulance often had to move at short notice so that sometimes all the larvae from a breeding-place were lost or destroyed in transit before any adults could be reared. Unfortunately, there was no material available for preserving larvae, so that it has been impossible to obtain specimens from many of the places studied.

Rainfall.

The figures given below are published by the Physical Department, Ministry of Public Works, Egypt (1922) and show the number of days with over 1·0 mm. of rain.

Judging from the few available records and information gathered from natives, the rainfall for the 1935–36 season was abnormally heavy. The ambulance left Addis Ababa on 25th December and reached Lake Ashangi (near Quoram) on 2nd March. Throughout this period rain fell on most days and heavy storms were quite common. One European who had lived at Dessie for 7 years stated he had only experienced such weather in Abyssinia during the height of the rainy season.

	Addis Ababa (1908–1920)	Dessie (1908–1915)	Quoram (1908–1915)
January	2·6	1·0	2·3
February	4·8	5·3	4·0
March	6·9	8·0	7·0
April	9·5	9·0	8·0
May	7·5	10·1	7·7
June	17·0	4·6	3·2
July	26·6	18·0	18·1
August	25·8	19·1	20·9
September ...	19·5	12·1	8·8
October	2·8	3·9	4·8
November... ...	1·2	1·4	2·1
December ...	1·3	2·2	3·5

Description of Breeding-places.

(1). Dessie, 8,600 feet, 28.xii.1935 to 14.x.1936.

The town consisted of native huts with a few scattered houses of European design and straggled through an undulating valley for two or three miles. Apart from eucalyptus trees which were to be found in every compound and were almost the only source of shade, the country was barren, little cultivated and covered with short grass. In and around the town, the chief sources of mosquito breeding were small collections of water which had seeped out from the sides of the surrounding hills ; in addition, breeding was taking place along the edges of a little river which ran swiftly round the north and eastern parts of the town. This river had cut a winding rocky channel for itself and many pools were left from the flood water of the rainy season. At one spot the main route to the north crossed the river, with the result that the locality provided the water supply and the latrine space for a large section of the town. Two small pools about 1 foot to 18 inches deep, formed by depressions in the rocks, were particularly studied (Plate IX, fig. 1). The water was a turbid green colour, had a foul putrid smell, and judging by the vicinity, was highly contaminated with human excrement. The pools contained no vegetation other than algae and the water and surrounding rocks were in full sunlight. Enormous numbers of pupae and Anopheline and Culicine larvae were found in these pools, in far greater concentration than in any other breeding-place examined during this investigation. Samples taken on 30.xii.1935 yielded *Anopheles garnhami*, Edw. (2 ♂♂, 1 ♀), *Anopheles christyi*, N. & C. (1 ♂) and *Culex andersoni*, Edw. (7 ♂♂, 8 ♀♀).

In the centre of the town, water, seeping out of the side of the hill, collected in ditches at the edge of the road where it formed little shallow puddles of slightly turbid water (Plate IX, fig. 2). The bordering grass was the only source of shade. *Culex andersoni*, Edw. (5 ♂♂, 7 ♀♀) were reared from larvae collected on 30.xii.1935.

A muddy road at the south-west extremity of the town followed the course of an irrigation channel which, owing to the recent rains, had overflowed across the road forming collections of turbid water in the numerous hoof-marks. The puddles contained no vegetation and were in full sunlight. Larvae and pupae collected on 14.i.1936 were found to be *Culex andersoni*, Edw. (3 ♂♂, 3 ♀♀).

(2). Garado Valley, *circa* 8,000 feet, about 3 miles west of Dessie, 14.i.1936.

This valley was entered by passing through a short gorge at the south-west end of the town. It consisted of a perfectly flat plain about 1 to 2 miles broad, running in a north-westerly direction, and surrounded by steep mountains rising up to approximately another 1,000 feet. Numerous irrigation channels, fed from the mountain streams, transected the plain and eventually flowed into a little river which ran through the valley. One irrigation channel about 2 to 3 ft. wide and a foot deep contained clear running water (Plate IX, fig. 3). The edges were lined with grass and here, protected from the main current, larvae and pupae were found. *Anopheles garnhami*, Edw. (2 ♂♂) and *Culex theileri*, Theo. (2 ♂♂, 1 ♀) were reared from the samples taken.

Numerous small grassy pools had been formed by the recent rains and contained stagnant but clear water which was only a few inches deep. Pupae and many Anopheline and Culicine larvae were found amongst the grass. Only *Anopheles christyi*, N. & C. (1 ♀) was reared from the samples collected.

One old irrigation channel was completely overgrown with tall grasses and contained stagnant, slightly turbid water which was only about 2 inches deep. *Anopheles garnhami*, Edw. (1 ♂, 1 ♀) were reared from the larvae collected.

Much of the plain was tilled with a rough wooden plough which left small depressions in the ground ; these had filled with water, forming slightly turbid puddles bare of vegetation. Anopheline and Culicine larvae were collected from this breeding-place but only *Aëdes quasiunivittatus*, Theo. (1 ♀) was reared.

In this valley many small villages were found on the mountain sides but not a hut was to be seen within about 300 ft. of the plain, although the latter was either cultivated or pasture land. Valleys of this description were often seen in northern Abyssinia, but this was the only occasion when it was possible to study their mosquitos. The natives associate the river valleys with " fever " and on no occasion was a camp found at the side of a stream. This system often necessitated water having to be carried long distances.

(3). Waldia, *circa* 6,000 ft., 25.i.1936 to 27.i.1936.

The camp was situated about 2 miles west of Waldia on the road to Lalibela and within about 200 yds. of the Tikurwoha River. The hills on each side ran steeply down to the river-bed, which was from 100 to 300 yds. wide and covered with loose stones and boulders. Apart from the main stream there were many little streams, often with clear pools and backwaters, threading their way amongst the rocks. It was these small collections of water that formed the mosquito breeding-places. It appeared that during the height of the rainy season the whole river-bed would contain one vast torrent and the numerous breeding-places would be destroyed. A few rocky pools of clear water contained quantities of *Spirogyra*, under which were found Anopheline and Culicine larvae from which was bred *Culex annulioris*, Theo. (1 ♀).

Running between the stones of the river-bed was a stream of clear water not more than a foot wide. Culicine larvae and many pale green Anopheline larvae were found completely hidden from view by thick masses of *Spirogyra* which grew from the bordering stones. *Anopheles cinereus*, Theo. (2 ♂♂, 3 ♀♀) were bred from the specimens collected on 27.i.1936.

(4). Lake Ashangi, 15.iii.1936.

By this date what was left of the Ambulance was hidden in a cave in the mountains about 3 miles south-west of Lake Ashangi at a height estimated at well over 9,000 ft. The locality was usually shrouded in mist for the greater part of the day and the weather was cold and damp. The maximum and minimum temperatures recorded under the eaves of a tent were 63°F. and 44°F. respectively. There were numerous small mountain streams in the neighbourhood which ran precipitously down to the Ashangi Plain over 1,000 ft. below. These streams had numerous little pools of clear, constantly moving water ; at the edges great numbers of larvae and pupae were found under the shade of the overlying rocks and vegetation. *Anopheles garnhami*, Edw. (1 ♀) and *Culex andersoni*, Edw. (1 ♀) were bred from these larvae.

A very few adult mosquitos were caught. *Anopheles garnhami*, Edw. (1 ♀) and *Culex andersoni*, Edw. (2 ♂♂, 1 ♀) were captured in the camp at Dessie ; *Culex andersoni*, Edw. (1 ♀) in the camp in the grounds of the British Legation, Addis Ababa ; and *Culex annulioris*, Theo. (1 ♀) near breeding-places within 400 yards of the Waldia camp.

Of the 61 specimens that have been identified, 55 were reared from larvae or pupae. They include 7 different species, 4 of which, *Anopheles cinereus*, Theo., *Anopheles christyi*, N. & C., *Anopheles garnhami*, Edw. and *Culex annulioris*, Theo., so far as I am aware, have not previously been recorded from Abyssinia.

Malaria.

None of the species recorded has proved to be susceptible to infection with the malaria parasite, and it seems more than likely that the absence of *A. costalis* in particular is an omission due to so few breeding-places being examined and to the difficulties of rearing adults. This species has been reported from Central Abyssinia by Scott (1927) and Symes (1928) has described it breeding together with *A. cinereus*, Theo., and *A. christyi*, N. & C., in Kenya ; his account of the breeding-places of the latter species in highly contaminated water and the suggestion that the albuminoid ammonia content is a factor determining the distribution of this species, explain the concentration of larvae found at Dessie. The same author (1930) has suggested that *A. christyi* and *A. cinereus* are attracted especially to cattle and that comparatively few specimens are found in dwellings. This might account for these species not being caught in the camps, as an enormous number of domestic animals, chiefly mules, were usually to be found in the vicinity.

Little definite information could be obtained regarding the distribution of malaria in Northern Abyssinia. Two cases with *P. falciparum* infection were observed in Abyssinian soldiers in Dessie ; one of these cases had an acute attack and had been in the vicinity for at least 3 weeks. At Waldia, Macfie (1936) observed 20 cases of malaria out of 989 patients who attended the Ambulance for treatment ; a number of these cases, however, were not confirmed by the microscope. The 15 European members of the Unit rarely used mosquito nets, but 5 grains of quinine were taken daily ; no proved cases of malaria occurred, although at least one member of the Unit developed an unexplained pyrexia, which, however, did not react to quinine. The only other figures I have been able to obtain are those of Chabaneix (1901) who was a member of the Medical Mission which accompanied the French Minister to Addis Ababa in 1897. In a series of about 8,000 cases he reports that 3·69 per cent. were diagnosed as malaria, quartan fever being the least common. Unfortunately it was found impossible to determine the splenic index in any of the areas visited by the Ambulance, but it was noticed that children were not pot-bellied, as was the case in West Africa. The impression gained was that malaria was not endemic in the highlands of Northern Abyssinia ; sporadic cases occurred, but they were probably due to relapses from old infections contracted at lower altitudes.

Mosquitos reported from Abyssinia.

Anopheles garnhami, Edwards.

Loc. Dessie, 8,600 ft., 30.xii.1935, 2 ♂♂, 1 ♀, larvae and pupae abundant in rocky pools highly contaminated by sewage near river; 7.i.1936, 1 ♀, gorged with blood, caught in camp. Garado Valley, *circa* 8,000 ft., 14.i.1936, 2 ♂♂, larvae and pupae at grassy edges of a swiftly flowing irrigation channel; 1 ♂, 1 ♀, larvae in stagnant overgrown irrigation channel. Lake Ashangi (mountains 3 miles to the south-west), *circa* 9,000 ft., 15.iii.1936, 1 ♀, larvae in clear mountain stream. Yerga Alem, Sidamo Province, 1 ♀ (very small specimen) (*Dr. Harriet Nystrum*).

Anopheles cinereus, Theobald.

Waldia (Tikurwoha river-bed), *circa* 6,000 ft., 27.i.1936, 2 ♂♂, 3 ♀♀, numerous larvae in clear stream with *Spirogyra*. Addis Ababa, 9 ♂♂, 5 unfed ♀♀ in house; Lalibela, 1 ♀. Yerga Alem, Sidamo Province, 1 ♀ (*Dr. Harriet Nystrum*).

Anopheles christyi, N. & C.

Dessie, 8,600 ft., 30.xii.1935, 1 ♂, larvae in rocky pools contaminated with sewage. Garado Valley, *circa* 8,000 ft., 1 ♀, 14.i.1936, larvae at grassy edges of pools formed by flood water.

Anopheles gambiae, Giles (*costalis*, Theobald).

Yerga Alem, Sidamo Province, 4 ♀♀ (*Dr. Harriet Nystrum*). Doukham, about 20 miles south-east of Addis Ababa, *circa* 6,500–7,000 ft., 1 ♀ (*Dr. H. Scott*). Muger River, 30 miles north of Addis Ababa, *circa* 5,500 ft., 1 ♀ (*Scott*).

Anopheles coustani, Lav., var. *ziemanni*.

Berga River, nearly 30 miles due west of Addis Ababa, *circa* 7,500 ft., 4 ♀♀ (*Scott*). Lakkidamba, edge of swamp on north-east shore of Lake Zwai, *circa* 5,500 ft., 8 ♀♀ (*Scott*). Bahrdar Giorgis, at the southern extremity of Lake Tana, specimens collected by the Mission of 1920–21. Various localities on borders of Lake Tana (*Major Cheesman*).

Anopheles mauritianus, Grp., var. *paludis*, Theo.

On the banks of the River Pibor (*Balfour*).

Anopheles pharoensis, Theobald.

Makki River, north-west of Lake Zwai, *circa* 5,500 ft., 1 ♀ (*Scott*). Borders of Lake Tana (*Major Cheesman*). Lakkidamba, edge of swamp on north-west shore of Lake Zwai, *circa* 5,500 ft., 47 ♀♀ (*Scott*). River Baro (*Balfour*).

Anopheles transvaalensis, Carter (?).

British Legation at Addis Ababa, *circa* 8,000 ft., 1 ♂ (*Scott*).

Anopheles squamosus, Theobald.

Bahrdar Giorgis, specimens collected by Mission to Lake Tana of 1920–21.

Anopheles wellcomei, Theobald.

On the banks of the Baro and Pibor Rivers (*Balfour*).

Anopheles funestus, Giles.

Yerga Alem, Sidamo Province, 1 ♀ (*Dr. Harriet Nystrum*). On the banks of the Baro and Pibor Rivers (*Balfour*).

Anopheles marshalli (? type form or var. *gibbinsi*).

Wando, near Lake Awusa, 5,400 ft. (*Dr. Harriet Nystrum*). Yerga Alem, Sidamo Province (*Nystrum*).

Culex andersoni, Edwards.

Dessie, 8,600 ft., 30.xii.1935, 7 ♂♂, 8 ♀♀, larvae abundant in rocky pools contaminated with sewage, 5 ♂♂, 7 ♀♀, larvae found in roadside ditch ; 3 ♂♂, 3 ♀♀, larvae in muddy hoof marks. Addis Ababa, grounds of British Legation, 8,000 ft., 24.xii.1935, 2 ♀♀ caught in camp ; 1 ♂ caught by Scott and specimens recorded by Dr. Harriet Nystrum from same town. Lake Ashangi (mountains 3 miles to south-west), over 9,000 ft., 1 ♀, larvae found in clear mountain stream. Mulu, above the Muger Valley, 30 miles north of Addis Ababa, 1 ♂ (*Scott*). Lalibela (*Dr. Harriet Nystrum*).

Culex pipiens, L.

Doukham, 20 miles south-east of Addis Ababa, 6,500–7,000 ft., 1 ♂ (*Scott*). Addis Ababa (*Dr. Harriet Nystrum*). Borders of Lake Tana (*Major Cheesman*).

Culex poecilipes, Theobald (*quasigelidus*).

Bahrdar Giorgis, specimens collected by Lake Tana Mission of 1920–21. Borders of Lake Tana (*Major Cheesman*).

Culex theileri, Theobald.

Garado Valley, near Dessie, *circa* 8,000 ft, 2 ♂♂, 1 ♀, larvae at edges of clear water in irrigation channel. Mount Zukwala, 40 miles south of Addis Ababa, over 9,000 ft., 4 ♀♀ (*Scott*). Hora Harsadi, Lakes of Addas, some 25 miles south-east of Addis Ababa, *circa* 7,500 feet, 1 ♀ (*Scott*).

Culex vansomereni, Edwards.

Berga River, a few miles beyond Addis Allem, 30 miles due west of Addis Ababa, *circa* 7,500 ft. 3 ♀♀ (*Scott*). Djem-Djem Forest, some 45 miles west of Addis Ababa, *circa* 8,000 feet, 1 ♂ (*Scott*). Addis Ababa, 1 ♂, 1 ♀ (*Scott*) ; specimens recorded from the same town by Dr. Harriet Nystrum.

Culex annulioris, Theobald.

Waldia, *circa* 6,000 feet, 25.i.1936, 1 ♀, larvae found in clear pools with masses of *Spirogyra* ; 1 ♀ caught at night near this breeding-place.

Culex guiarti, Blanchard.

Banks of Baro and Pibor Rivers (*Balfour*).

Culex rubinotus, Theobald.

Wando, near Lake Awusa (*Dr. Harriet Nystrum*).

Culex fatigans, Wiedmann.

On the banks of Baro and Pibor Rivers (*Balfour*).

Culex antennatus, Becker.

Borders of Lake Tana (*Major Cheesman*).

Culex bitaeniorhynchus, var. *tenax*, Theobald.

On the banks of Baro and Pibor Rivers (*Balfour*).

Culex tigripes, Grandpré.

Lalibela (*Dr. Harriet Nystrum*).

Culex sp. or spp.

Djem-Djem Forest, some 45 miles west of Addis Ababa, *circa* 9,000 ft., 1 ♀ indeterminable ; Lakkidamba, the swamp on the north-west shore of Lake Zwai, *circa* 5,500 feet, 1 ♀ indeterminable (*Scott*).

C. (*Lutzia*) *tigripes*, var. *fusca*.

Lalibela (*Dr. Harriet Nystrum*).

Aëdes (*Aëdimorphus*) *dentatus*, Theobald (?)

Forest of Mount Chillalo, some 20 miles east of Lake Zwai, *circa* 9,000 ft., 4 ♀♀ (*Scott*).

Aëdes quasiunivattus, Theobald.

Garado Valley, near Dessie, *circa* 8,000 ft., 14.i.1936, 1 ♀, larvae found in puddles in tilled land. Djem-Djem Forest, some 45 miles west of Addis Ababa, *circa* 9,000 ft., 2 ♂♂, 5 ♀♀ (*Scott*). Mulu, above the Muger River Valley, 30 miles north of Addis Ababa, *circa* 8,000 ft. 1 ♀ (*Scott*).

Aëdes africanus, Theobald.

Sidamo Province, 5,900 ft. (*Dr. Harriet Nystrum*).

Aëdes aegypti, Linnaeus.

On the banks of the River Pibor (*Balfour*).

Aëdes domesticus, Theobald (*Uranotaenia domestica*).

On the banks of the River Pibor (*Balfour*).

Taeniorhynchus (*Mansonioides*) *africanus*, Theobald.

North-west shore of Lake Zwai, *circa* 5,500 ft., 2 ♀♀ (*Scott*).

Taeniorhynchus (*Mansonioides*) *uniformis*, Theobald.

North-west shore of Lake Zwai, *circa* 5,500 ft., 3 ♀♀, Lakkidamba, edge of swamp on the shores of Lake Zwai, 7 ♀♀, near the marshes of Jilli, between Lake Zwai and Addis Ababa, *circa* 6,000 ft., 1 ♀ (all *Scott*). Bahrdar Giorgis, specimens collected by Lake Tena Mission of 1920–21. On the borders of Lake Tana (*Major Cheesman*). On the banks of the River Pibor (*Balfour*).

Taeniorhynchus (*Mansonioides*) *fuscopennatus*, Theobald.

Wanda, near Lake Awusa (*Dr. Harriet Nystrum*).

Taeniorhynchus (*Mansonioides*) *cristatus*, Theobald.

On the banks of the River Pibor (*Balfour*).

Uranotaenia balfouri, Theobald.

On the banks of the River Pibor (*Balfour*).

Ficalbia (*Eteroleptiomyia*) *mediolineata*, Theobald.

On the banks of the River Pibor (*Balfour*).

I wish to thank Sir Guy A. K. Marshall, F.R.S., of the Imperial Institute of Entomology, for his kind assistance. I am indebted to Dr. F. W. Edwards for the identification of the mosquitos and for the list of those collected by Major Cheesman and the CULICINI of Dr. Nystrum; for the ANOPHELINI collected by the latter I wish to thank Dr. A. M. Evans. I am also very much indebted to Dr. J. W. S. Macfie for his valuable help and advice.

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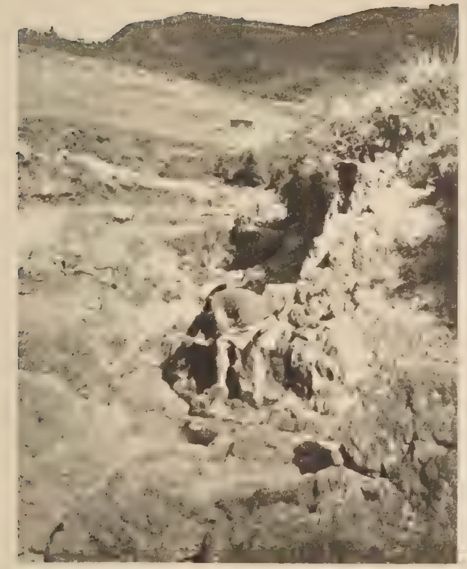

Fig. 1. Dessie. Rocky pools of water highly contaminated with sewage and containing larvae of *A. garnhami, A. christyi* and *C. andersoni.*

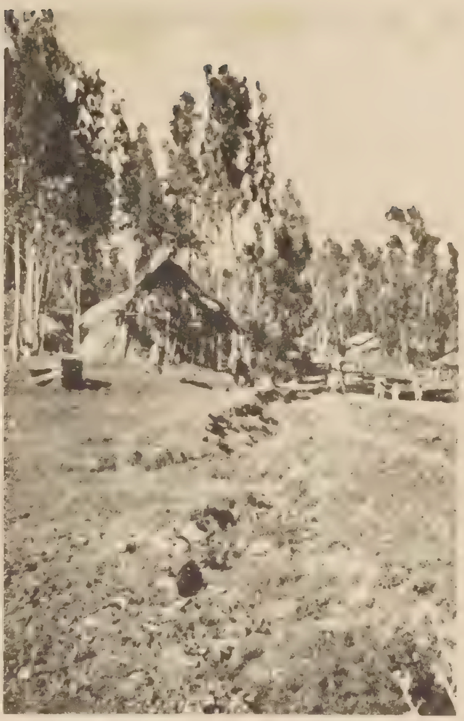

Fig. 2. Dessie. Roadside ditch in centre of town containing *C. andersoni* larvae

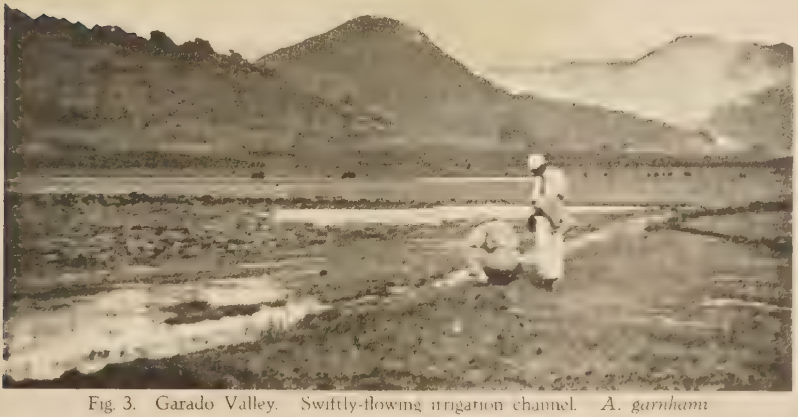

Fig. 3. Garado Valley. Swiftly-flowing irrigation channel. *A. garnhami* and *C. theileri* larvae found at edges.

SIMULIIDAE OF THE BUGANDA, EASTERN AND WESTERN PROVINCES OF UGANDA.

14

By E. G. Gibbins.

Introduction.

Five years ago, when a study was commenced of the Simuliid fauna of Uganda, 24 species were known from the whole of Africa. To-day, Uganda can claim more than that number within its own boundaries. In fact 30 species are known to occur in the country. And yet it is probable that many more species remain to be discovered, particularly as the investigation has not included the Northern Province, which will undoubtedly prove to be one of the richest in *Simulium*, since within its confines are the River Nile and its many subsidiary tributaries. Quite a number of species found in Uganda occur in other parts of the African continent. Some extend their distribution over to the west and also to the east coast, while other species do not confine their range to the tropics and are found as far afield as the Transvaal and Natal in the Southern Hemisphere. Early observations (1934) indicated a specialised Simuliid fauna on each of the high mountains in Uganda, and while this may still be true in the case of some species, subsequent investigations have shown that several have a wider distribution.

The present contribution concludes the study of the large collection of Uganda Simuliidae referred to in an earlier publication (1934). It includes a description of the male, female, pupa and cocoon, and in one case the larva, of three new species. One of the species, *Simulium obscurum*, sp. n., is of particular interest on account of its unique breeding-place. It was discovered with the aid of the light of an electric torch breeding in almost total darkness in a mountain stream flowing through a rock cavern situated in the midst of dense forest. The female of *Simulium neavei*, Roubaud, is redescribed; this human blood-sucking species, of which the male and early stages are unknown, is a vicious biter and was taken in the Kijura district near Fort Portal in 1932. *Simulium neavei* is concerned in the transmission of *Onchocerca volvulus* in the Belgian Congo (1932) and also occurs in Kenya, where it has been associated with a skin disease (1922) which was undoubtedly onchocerciasis. The fly also occurs in Ankole, where Dr. S. A. Neave obtained his original specimens. In addition, the present paper gives further details of the female terminalia of *Simulium damnosum*, Theobald, from the type locality at Jinja in order that other workers may be able to determine accurately the biting sex of this widely distributed species. A note is also included on the pupal respiratory organ of *Simulium elgonensis*, Gibbins, from Kabale, and finally, a statement is given of the distribution of Simuliidae in the Buganda, Eastern and Western Provinces of Uganda together with brief notes on the breeding-places and blood-sucking habits of the female where they are known.

Simulium obscurum, sp. n.

Simulium obscurum closely resembles *S. taylori*, Gibbins, externally and in the female terminalia but differs strikingly in the male terminalia, particularly the coxite and clasper, and in the respiratory organ of the pupa. It also somewhat resembles *Simulium equinum* var. *mediterraneum*, Puri 1925, in the pupal respiratory organ; in each case the secondary filaments are similarly arranged, but whereas in *obscurum* they have a common base on either side, and the ventral and dorsal group differ both in size and sculpture, the filaments are separated at their base and do not exhibit any marked difference in var. *mediterraneum*. The species may be easily distinguished in the male terminalia on the shape of the anterior part of the phallosome and the relative size of the coxite and clasper (Edwards, 1923).

♀. Length 2·5 mm.; wing 3 mm.

Head. Vertex, front and clypeus slate-grey. Vertex covered with golden scales with marginal outstanding black hairs on either side; clypeus densely covered with long pale hairs. Antenna dark brown, scape and first flagellar segment ochraceous; the whole densely covered with the usual ash-grey pubescence. Palp: sensory spot large. *Thorax.* Mesonotum dull black, densely and uniformly covered with brassy scales. Scutellum with dense brassy scales and long, upright posterior

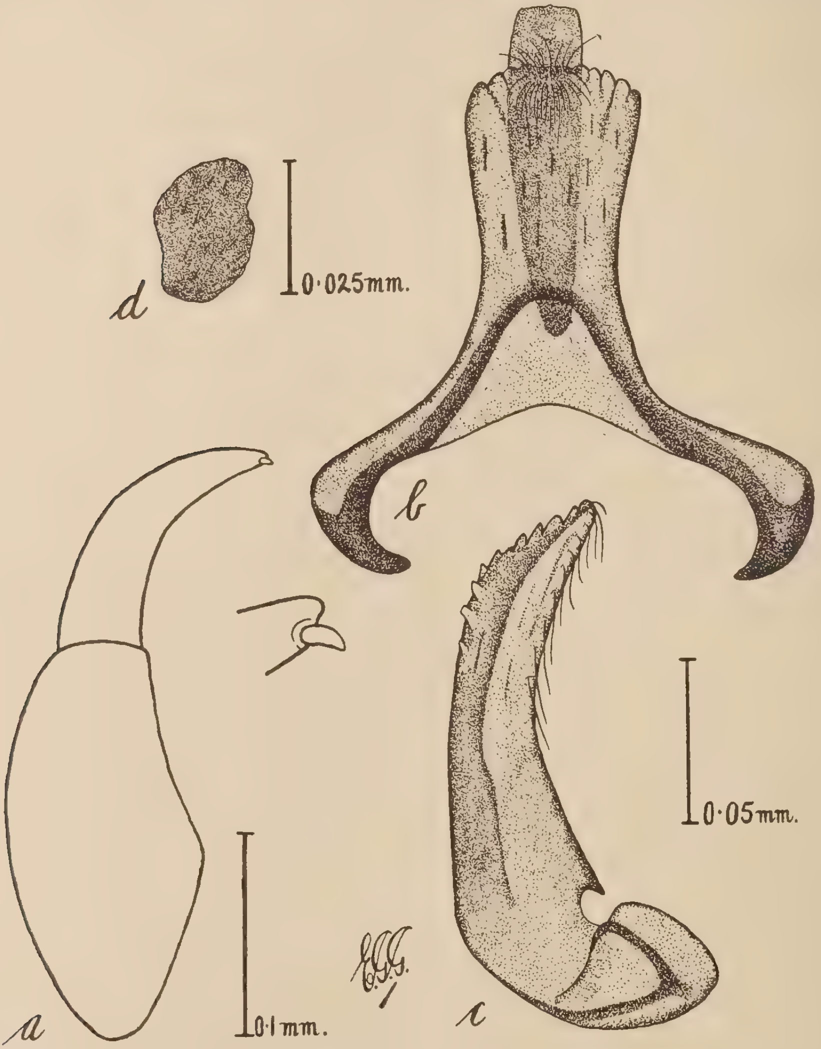

Fig. 1. *Simulium obscurum*, sp. n., male terminalia: *a*, ventral view of coxite and clasper, note tip of clasper enlarged to show sub-apical tooth; *b*, *c*, ventral and lateral views of the anterior part of the phallosome; *d*, cercus; (*b* and *c* drawn to the same magnification).

marginal hairs. Halteres pale yellow with brown stem. Pleura slate-blue, lacking patch of hairs on the membrane behind the thoracic spiracle. *Abdomen* black, with dense long narrow golden scales laterally and with dark brown scales on the dorsal surface of all but the first two segments which are covered with brassy scales; first tergite black with lateral fringe of yellow hairs of moderate length. *Terminalia* as in *S. touffeum* (fig. 3). *Legs* dark brown, basal quarter of hind and basal half of front femora with golden scales, mid femora sprinkled with golden scales; basal two-thirds of hind tibiae with yellow scales and front tibiae with silver scales. Hind first tarsal segment with a posterior yellow stripe. Calcipala present and pedisulcus distinct. Claws simple. *Wings* lacking basal cell, with dark hairs along almost the whole length of the subcosta and on the base of the radius.

♂. Length 2·5 mm.; wing 2·75 mm.

Head. Front and clypeus slate-grey, the latter with jet black upright hairs. Antenna dark brown. *Thorax.* Mesonotum velvet-black, densely and uniformly covered with brassy scales. Scutellum dark brown with dense, marginal, outstanding black hairs on the lateral posterior edge. Halteres very dark brown. Pleura as in female. *Abdomen* velvet-black, covered with long narrow deep brown scales, lateral surface and posterior half of dorsal surface of second segment grey, apical half of sixth and whole of seventh segment with a slate-grey lateral patch; first tergite black with dense lateral fringe of very long pale yellow hairs which are black towards their base. *Terminalia* (fig. 1): coxite (fig. 1 *a*) narrow, about half as long again as the clasper. Clasper long and narrow, tapering gradually in the distal half to a pointed tip which is armed with a subapical tooth on its lower edge. Phallosome: anterior part (fig. 1 *b*, *c*) in ventral view cylindrical, scalloped distally, with a median anterior patch of soft setae and with inwardly curved, heavily chitinised, downwardly projecting basal processes; in lateral view it is narrow and longer on its anterior side, which is covered with setae, in this position the basal processes appear triangular in shape; posterior part partly membranous, with large strong spines and a long apodeme. Cercus (fig. 1 *d*) small with short spines. Legs dark brown, femora and tibiae sprinkled with golden scales, tibiae of front legs with

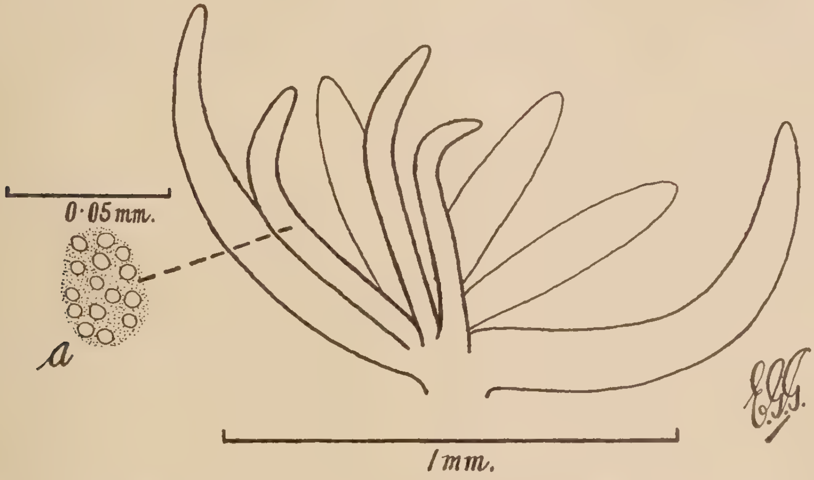

Fig. 2. *Simulium obscurum*, sp. n.; dorsal view of respiratory organ of pupa; *a*, part of outer wall enlarged to show sculpture.

basal two-thirds outwardly covered with dense yellow scales ; tarsi black. *Wings* as in female with the exception of the absence of hairs on the subcosta.

Holotype ♂, River Kisiwaki, Bufumbo, Mt. Nkokonjeru, 13.iv.32. Allotype ♀, same data. Paratypes 6 ♀♀, same data. Reared from pupae.

Larva. Similar to *S. taylori* but differing in the terminal teeth of the mentum which resemble those of *lepidum* (1936 c, fig. 13 *a*) in having the median tooth longer than the rest and the outer teeth with a shoulder on their inner edge.

Pupa. As in *S. taylori* with the exception of the respiratory organ (fig. 2). From the median area of a large semi-circular basal appendage arise six filaments ; three which leave the ventral surface are strong, upright and tubular with the basal two-thirds of the outer wall covered with disc-like tubercles (fig. 2 *a*), while the other three arising from the dorsal surface are fragile, semi-translucent, finger-like lobes which take up a horizontal position and lie on the anterior surface of the pupa.

Cocoon. As in *S. taylori.*

Breeding-places. The early stages of *S. obscurum* were obtained from the River Kisiwaki on the slopes of Mount Nkokonjeru not far from the rest camp of Bufumbo. They were attached to stones taken from small cascades in the river's course in association with the early stages of *S. dentulosum.* The river flows through forest and is heavily shaded and the fine tree roots dipping in the falls provided another means of anchorage. In one situation the stream flowed beneath a huge rock where in almost total darkness pupae were removed from a stone by the aid of the light of an electric torch.

Simulium touffeum, sp. n.

Closely resembling *Simulium lepidum* in having three dark stripes on the mesonotum, the male of *S. touffeum* is distinguishable by the presence of brassy scales on the thorax (these are pale yellow in *lepidum*) and in the dark lateral areas which appear as a broad stripe and merge with the median stripe posteriorly, whereas in *lepidum* these areas are oval and entirely isolated from the median stripe. The coxite and the anterior part of the phallosome when seen in ventral view are also strikingly different. In the female the species may be separated on the thoracic scales which are thinly disposed and brassy in colour, while in *lepidum* the mesonotum is covered with deep reddish brown scales with pale yellow scales anteriorly. The respiratory organ of the pupa is very distinct from that of *lepidum.*

♀. Length 3·5 mm. ; wing, 3·2 mm.

Head. Vertex, front and clypeus slate-grey ; vertex and front with sparse black hairs which are interspersed with sparse golden scales on the former, clypeus densely covered with pale hairs. Antenna dark brown with the exception of the scape, first and base of the second flagellar segment which are ochraceous. Palp : sensory spot large. *Thorax.* Mesonotum slate-blue with brassy scales and three black parallel stripes : a long narrow median stripe reaching from the anterior border to the scutellum and two short indistinct narrow stripes situated on either side extending from about the middle of the mesonotum to the scutellum. Scutellum slate-blue, densely covered with brassy scales which are longer than those on the thorax and interspersed with sparse long black hairs and with dense long yellow hairs along the posterior border. Pleura slate-grey without patch of hairs on the membrane behind the thoracic spiracle. Halteres yellow with brown stem. *Abdomen* dull black with dense yellow scales laterally ; first tergite brown, densely covered with outstanding yellow hairs interspersed with golden scales medially, lateral fringe of pale yellow hairs of moderate length. Second and third segments with sparse golden scales and fourth, fifth and sixth with reddish brown scales dorsally. Seventh and eighth segments metallic. *Terminalia.* Eighth sternite with a lightly chitinised median area bearing a deeply pigmented margin on either side. Anterior gonapophyses long and tapering almost to a point. Paraproct (fig. 3) with an inner anterior projection bearing stout bristles. Cercus heavily chitinised and rounded distally. *Legs* dark brown, front and hind femora sprinkled with golden scales ; basal two-thirds of front and hind tibiae and basal half of mid tibiae and first hind tarsal segment with yellow scales ; these are paler in colour on the front and mid tibiae. Calcipala present and pedisulcus distinct. Claws lacking basal tooth. *Wings* lacking basal cell, with dark hairs on the base of the radius and almost along the whole length of the subcosta.

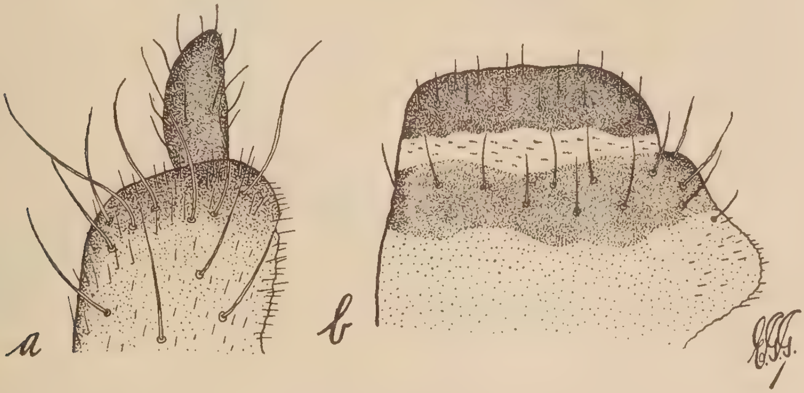

Fig. 3. *Simulium touffeum*, sp. n., female terminalia : paraproct and cercus ; *a*, lateral view ; *b*, ventral view. (Magnification as in fig. 1*a*.)

♂. Length 4 mm. ; wing 3·2 mm.

Head. Front and clypeus slate-grey, the latter with long outstanding black hairs. Antenna black, covered with the usual ash-grey pubescence. *Thorax.* Mesonotum velvet-black with brassy scales and long upright golden hairs posteriorly and with three large dark areas which are covered with short deep brown scales ; these are in the form of a long broad median stripe and one equally broad short stripe on either side, the lateral stripes are only separated from the median by a thin line of brassy scales and should the specimen have been rubbed the striped pattern may be lost. Scutellum densely covered with brassy scales interspersed with long, outstanding black hairs and golden hairs. Pleura slate-blue, lacking hairs on the membrane behind the thoracic spiracle. Halteres dark brown. *Abdomen* velvet-black, sparsely covered with dark brown scales ; first tergite black with dense lateral fringe of yellow hairs, many of which are very long. Second segment with a large slate-grey lateral patch sparsely covered with brown hairs, and sixth and apical border of fifth segment with a slate-grey lateral patch sparsely covered with black hairs. *Terminalia* (fig. 4). Coxite (fig. 4 *a*) less than twice the length of the clasper, about half its basal width apically and with an almost straight inner side when seen in ventral aspect. Clasper short, tapering suddenly in the anterior third with a small broad chitinised tooth at the tip. Phallosome resembling *lepidum* (1936 *c*) in lateral view but with a strikingly different anterior part when seen from a ventral aspect. Anterior part (fig. 4 *b*) narrow in ventral view, simulating an inverted Y with a flat and slightly expanded distal end bearing setae ; the downward projecting processes expand gradually near the base and terminate in a rounded end ; median process long and narrow. Cercus as in lepidum. *Legs* dark brown, basal two-thirds of front and basal half of hind tibiae with pale yellow scales ; hind legs with small spot of yellow scales at the base of the tibiae and with first tarsal segment large and

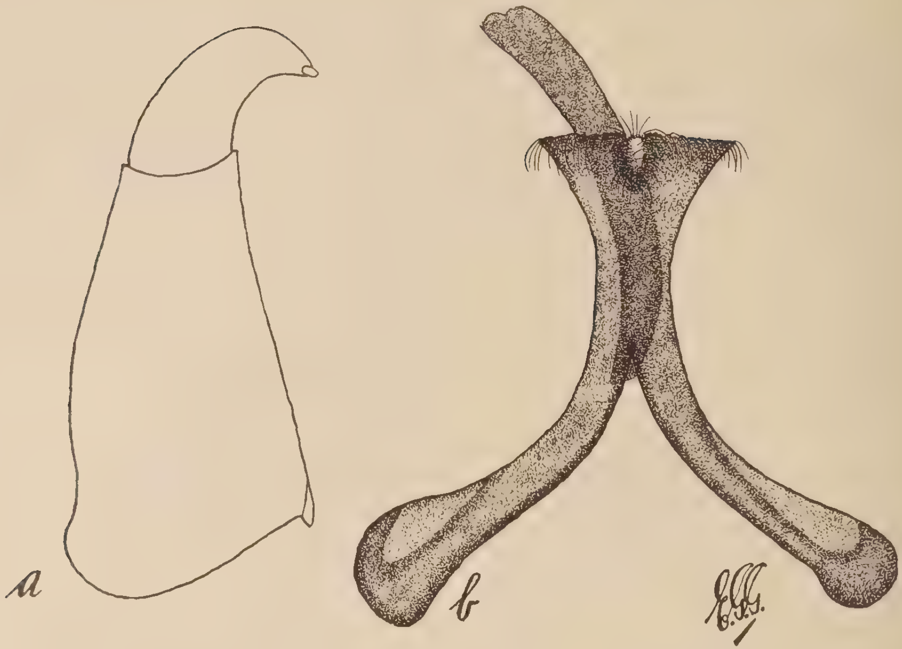

Fig. 4. *Simulium touffeum*, sp. n., male terminalia: *a*, ventral view of coxite and clasper; *b*, anterior part of phallosome in ventral aspect. (Magnification as in fig. 1 *c*.)

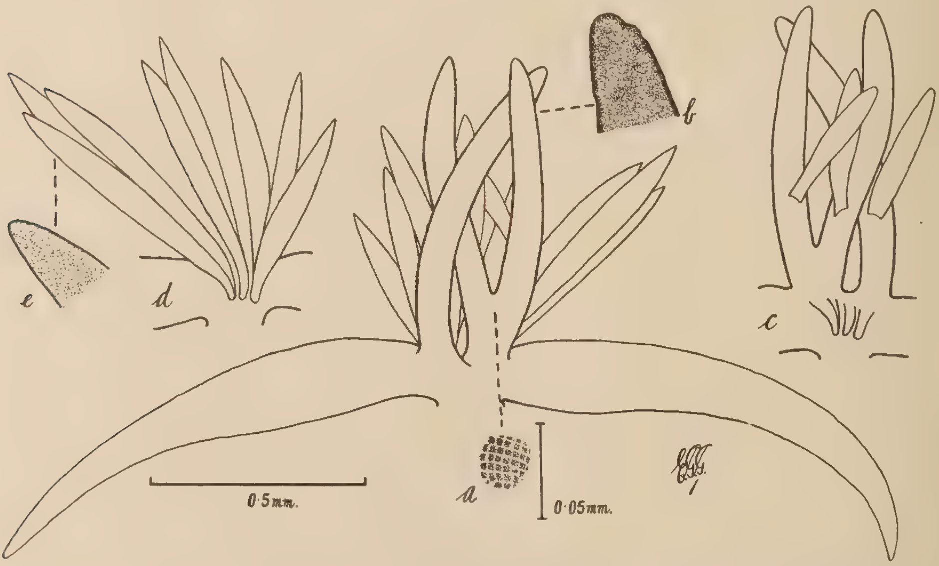

Fig. 5. *Simulium touffeum*, sp. n., dorsal view of respiratory organ of pupa: *a*, part of one of the main chitinised filaments enlarged to show sculpture of outer wall near the base; *b*, showing degree of chitinisation of anterior part of the above filaments; *c*, ventral view of the three main chitinised filaments showing the small finger-like processes on the ventral surface, bases of lancet-shaped filaments only are shown; *d*, ventral view of the median part of the organ showing the lancet-shaped filaments; *e*, showing the appearance of the outer wall of the above which is similar in the case of the main basal appendages. (*a*, *b*, and *e* to same magnification; *c* and *d* as in main figure.)

swollen medially. *Wings* as in female but with a basal cell and fewer hairs on the subcosta.

Holotype ♂, Sabei, Mt. Elgon, Uganda, 4.v.32. Allotype ♀, same data. Paratypes 4 ♂♂, 10 ♀♀, same data. Reared from pupae.

Larva. Unknown.

Pupa. Head and thorax with numerous disc-like tubercles, trichomes with four branches arising from a short stem. Respiratory organ (fig. 5) with two large and almost identical semi-translucent basal appendages which form a semi-circle round the head of the pupa and are situated on either side of a median tuft of 14 short filaments. These are arranged as follows: three filaments, two of which are paired and arise from a short broad stem, leave the dorsal surface and are chitinised (fig. 5 *a*) and bear a small semi-translucent finger-like process about the middle of their ventral surface (fig. 5 *c*). Eight more (fig. 5 *d*) with extremely fragile, lancet-shaped filaments arise ventrally and are closely arranged at the base and spread out fan-wise distally. *Abdomen* as in *lepidum*.

Cocoon of the common shape (as in the case of *S. hargreavesi*, 1934), 3·75 mm. in length, dark brown and gelatinous in texture.

Breeding-places. On Mount Elgon the pupa of *S. touffeum* was found in shaded parts of the River Sipi (6,000 ft.) in the clean spaces on stones covered with organic matter lying in about a foot of water. At Sabei in the River Kaptokoi (6,000 ft.) the early stages were found in heavy shade in company with the larvae of *S. elgonensis* on the clean surface of dark-coloured stones lying in about a foot of effervescent water below a small cascade.

Simulium octospicae, sp. n.

The species belongs to the group having a patch of hairs on the membrane behind the thoracic spiracle and is closely related to *S. kauntzeum* but is easily separated on account of its much smaller size. The male differs noticeably in the median process of the anterior part of the phallosome and the female in the paraproct, while the respiratory organ of the pupa is strikingly different.

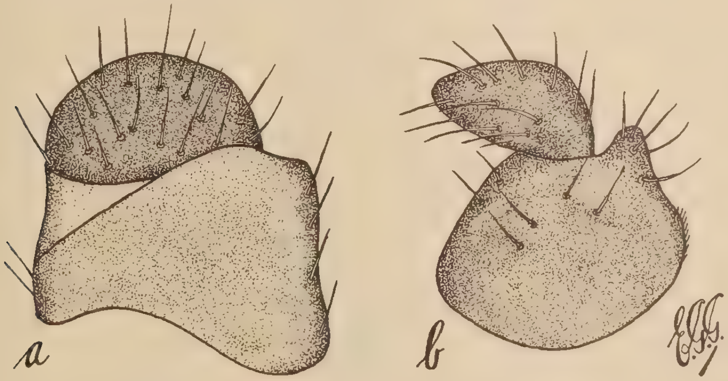

Fig. 6. *Simulium octospicae*, sp. n., female terminalia, paraproct and cercus: *a*, ventral view; *b*, lateral view. (Magnification of *a* as in fig. 1 *c*; *b* as in fig. 1 *a*.)

♀. Length 3·5 mm.; wing 3·1 mm.

Head. Vertex, front and clypeus slate-grey, sparsely covered with black hairs which are interspersed with golden scales on the vertex. Antenna dark brown with the exception of the scape and the first flagellar segment which are ochraceous.

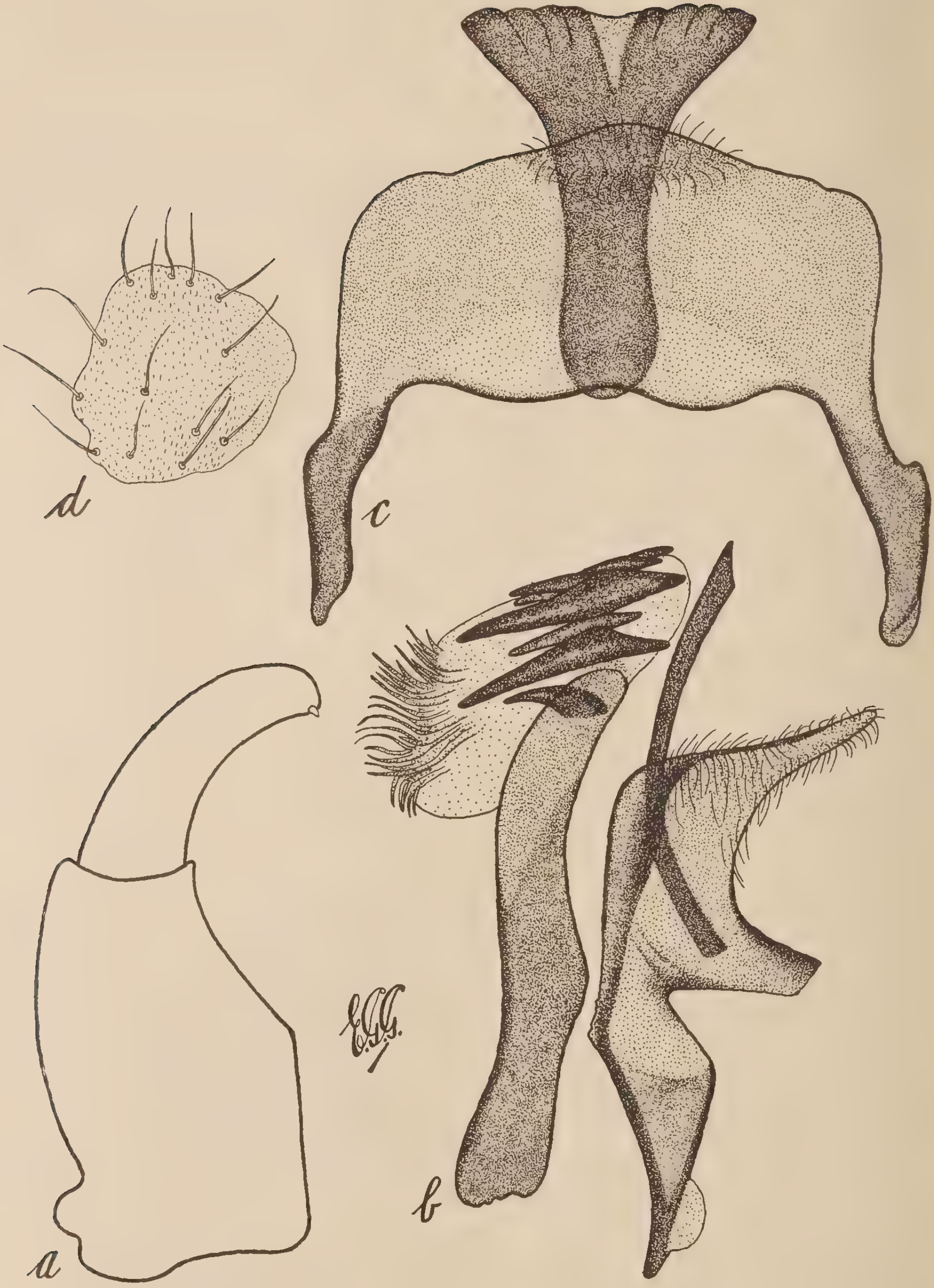

Fig. 7. *Simulium octospicae*, sp. n., male terminalia: *a*, ventral view of coxite and clasper; *b* phallosome in lateral view; *c*, anterior part of phallosome in ventral view; *d*, cercus. (Magnification of *a* as in fig. 1*a*; *b*, *c* and *d* as in fig. 1*c*.)

Thorax. Mesonotum dull black, covered with golden scales. Pleura slate-blue with patch of soft yellow hairs on the membrane behind the thoracic spiracle. Scutellum brown with golden scales and long outstanding pale marginal hairs. Halteres pale yellow. *Abdomen* dark brown, covered with golden scales which are sparse on the sixth, seventh and eighth segments ; first tergite light brown with lateral fringe of short yellow hairs. Spermatheca sub-spherical, unsculptured and heavily chitinised. *Terminalia.* Eighth sternite with a lightly chitinised median area. Anterior gonapophyses densely covered with fine setae with a long tapering entirely bare distal end. Paraproct (fig. 6) narrowly chitinised anteriorly with a finely spiculate, unchitinised inner process which is somewhat difficult to discern.

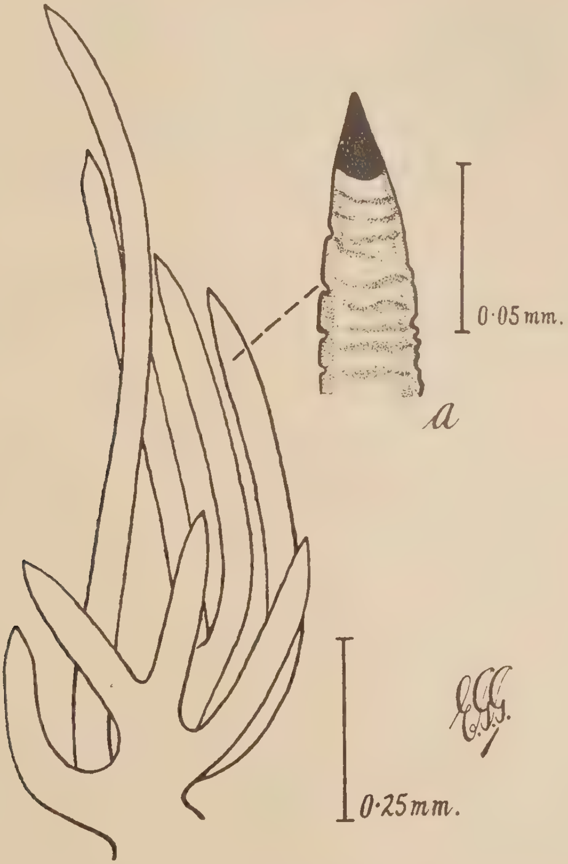

Fig. 8. *Simulium octospicae*, sp. n., ventral view of respiratory organ of pupa: *a*, distal end of filament enlarged to show appearance of outer wall.

Cercus small. *Legs* dark brown ; femora sprinkled with yellow scales, basal two-thirds of mid and hind tibiae with pale yellow scales and front tibiae with silver scales ; posterior basal half of hind first tarsal segment yellow with the exception of a small dark spot at the base. Calcipala present and pedisulcus distinct. Claws with a well-developed basal projection. *Wings* lacking basal cell, with dark hairs on the base of the radius and subcosta.

♂. Length 3·5 mm. ; wing 3 mm.

Head. Front and clypeus slate-grey, the latter thickly covered with black upright hairs. Antenna dark brown. *Thorax* velvet-black with golden scales. Pleura as in female. Scutellum black with dense long narrow golden scales and long outstanding marginal hairs which are more thickly placed laterally. Halteres dark brown. *Abdomen* velvet-black sparsely covered with brassy scales ; first tergite dark brown with lateral fringe of long pale yellow hairs. *Terminalia* (fig. 7). Coxite (fig. 7 *a*) about half as long again as the clasper ; in ventral aspect its inner side is equally divided into an upper concave and a lower straight edge. Phallosome (fig. 7 *b*) : anterior part in ventral view (fig. 7 *c*) broad with setae covering the median anterior area, in lateral aspect with a long, narrow, anterior process thickly covered with setae ; median process large and Y-shaped with a scalloped distal edge ; posterior part partly membranous with large deeply chitinised and backwardly projecting spines, apodeme long and broad. Cercus (fig. 7 *d*) circular and lightly chitinised with stout bristles arranged irregularly over its surface. *Legs* dark brown, basal half of hind and mid tibiae with pale yellow scales, basal two-thirds of front tibiae covered with silver scales outwardly, first hind tarsal segment large and swollen sub-apically. *Wings* as in female, but lacking hairs on the subcosta.

Holotype ♂, Bumboi, Bugishu, Uganda, 13.iv.32. Allotype ♀, same data. Reared from pupae.

Larva. Unknown.

Pupa. Head and thorax with sparse disc-like tubercles and simple trichomes. Respiratory organ (fig. 8) composed of four long and four short strong filaments which have deeply pigmented tips and a finely striated outer wall (fig. 8 *a*). In each case the middle pair unite at a short distance above the base, forming a broad stem. The shorter row of filaments lie in a ventral position. Abdomen as in *S. touffeum.*

Cocoon as in *S. touffeum.*

Breeding-places. Only two pupae of *S. octospicae* were obtained, which yielded the two adults described above. One was taken in association with *S. lepidum* and *S. brachium* in the River Nabigwo at about 6,000 ft. and the other in company with *S. simplex* and *S. masabae* in the River Kyagodo at a similar altitude. In both places the pupae were obtained from fine tree roots which were dangling in the spray at the side of waterfalls situated in well shaded parts of the river.

Simulium neavei, Roubaud.

The female of *S. neavei* was briefly described by Roubaud in 1915 from specimens collected by Dr. S. A. Neave in Western Ankole. The species is redescribed from five examples taken beside a forest stream in the Kijura district near Fort Portal in the act of biting on 16th October, 1931.

♀. Length 2·5 mm. ; wing 2·5 mm.

Head. Vertex, front and clypeus slate-grey with pale yellow scales. Labrum-epipharynx : terminal hooks, each pair with three heavily chitinised hooks ; in ventral view (fig. 9 *a*) the median hook is difficult to discern but in a lateral aspect (fig. 9 *b*) it can be clearly seen. Antenna black, scape and first flagellar segment brown. Palp with small circular sensory spot. *Thorax.* Mesonotum dull black, uniformly and densely covered with golden scales. Scutellum dull black, densely covered with long narrow golden scales and with golden upright hairs along the posterior border ; on either side at the lateral extremity these hairs are arranged in the form of a tuft. Pleura slate-blue, lacking patch of hairs on the membrane behind the thoracic spiracle. Halteres yellow. *Abdomen* dull black, densely and uniformly covered with golden scales on both the dorsal and lateral surfaces ; first tergite black with lateral fringe of yellow hairs of moderate length. Tergal plates of 3rd, 4th and 5th segments small. Spermatheca sub-spherical, heavily chitinised and unsculptured ; duct and posterior end unchitinised. *Terminalia.* Eighth sternite with a slightly depressed median area, lacking setae and chitinised to the same degree as the rest of the segment. Anterior gonapophysis (fig. 9 *e*) small, rounded and spiculate with about four large spines. Paraprocts (fig. 9 *c*) oval in ventral aspect and armed with stout bristles on the inner edge ; when seen in lateral view (fig. 9 *d*) the inner side shows no projection. Cercus narrow with flat distal edge when viewed laterally. *Legs* dark brown ; front legs with basal half of femora

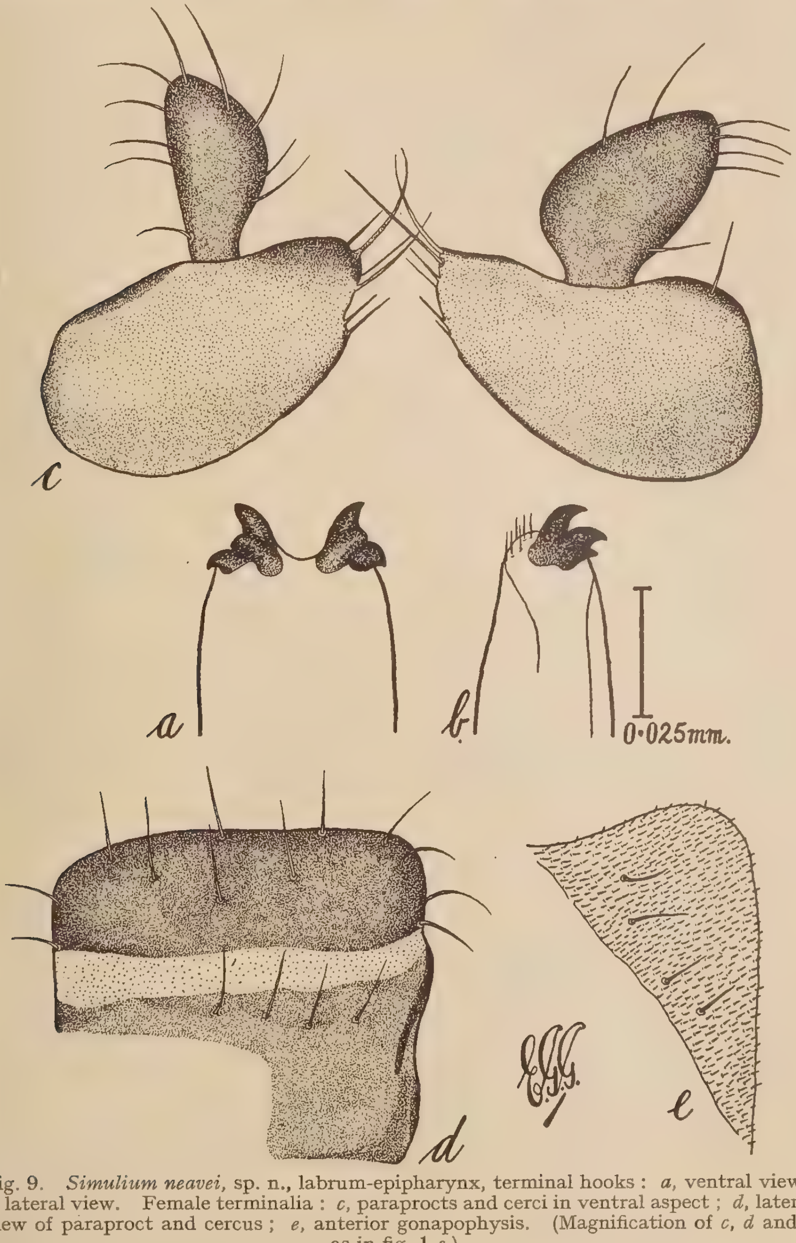

Fig. 9. *Simulium neavei*, sp. n., labrum-epipharynx, terminal hooks : *a*, ventral view ; *b*, lateral view. Female terminalia : *c*, paraprocts and cerci in ventral aspect ; *d*, lateral view of paraproct and cercus ; *e*, anterior gonapophysis. (Magnification of *c*, *d* and *e* as in fig. 1 *c*.)

and outward basal two-thirds of tibiae with yellow scales. Middle legs with basal third of hind femora and basal two-thirds of tibiae with yellow scales. Hind legs with basal two-thirds of femora and basal half of tibiae with yellow scales ; basal half of first tarsal segment with a posterior yellow stripe. Claws simple. *Wings* with basal cell, a few hairs on the subcosta and hairs on the base of the radius.

Simulium damnosum, Theobald.

In a previous contribution (1933) the writer illustrated the female terminalia of *S. damnosum* from a posterior aspect. Further studies have shown that the most advantageous method of depicting the main diagnostic features of the female terminalia of *Simulium* is in a lateral and ventral aspect. With the exception of *damnosum* this manner of illustrating the female terminalia has been adhered to throughout a series of publications on the subject and it is intended to rectify the omission below. Recently (1935) the male terminalia of *damnosum* were figured in detail.

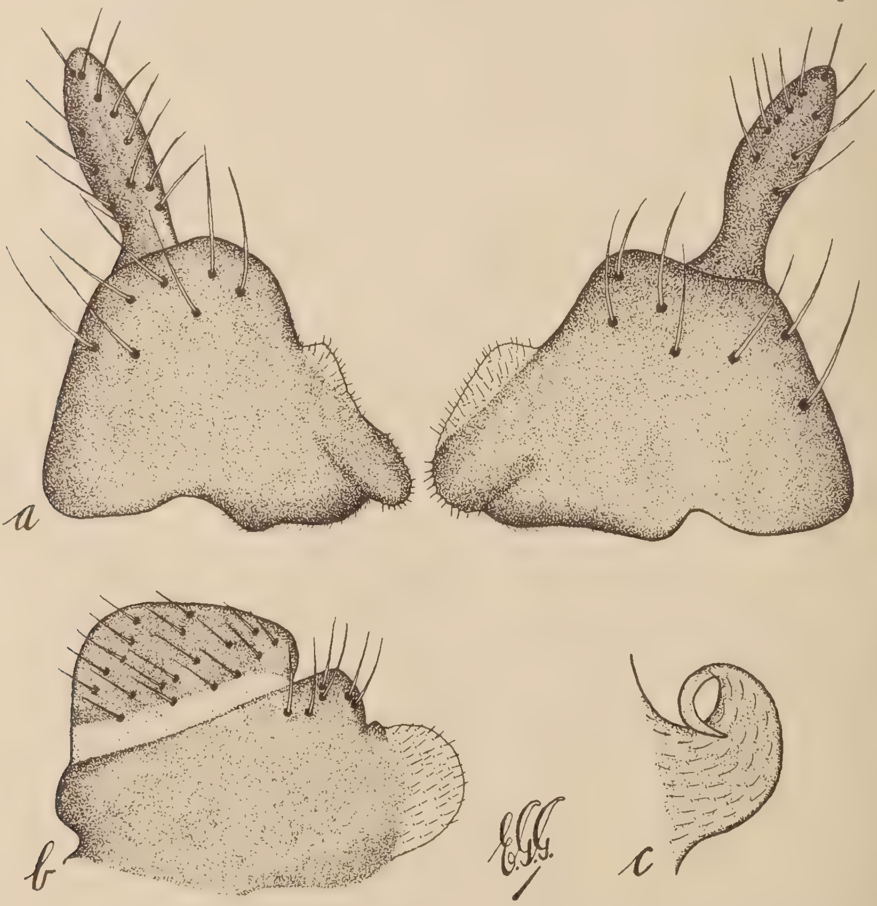

Fig. 10. *Simulium damnosum.* Female terminalia : *a*, ventral view of paraprocts and cerci, *b*, lateral view of paraproct and cercus, *c*, anterior gonapophysis. (Magnification of *a* and *b* as in fig. 1 *c* ; *b*, as in fig. 1 *a*.)

It may be mentioned here that an examination of a dissected and mounted wing of *S. damnosum* has shown a discrepancy in the wing drawn from a pinned specimen and illustrated in the previous study of the species (1933). The anterior venation should have been shown as depicted in the case of *S. adersi* (1934, p. 55, fig. 2) and not with R_1 and Rs fused distally as shown on page 46.

Abdomen. Tergal plates large, covering the dorsal surface of all segments. *Terminalia* (fig. 10). Anterior gonapophysis (fig. 10 *c*) long and tapering. Paraprocts (fig. 10 *a*) in ventral view large and wider proximally than distally with a downwardly directed inner chitinised process armed with small setae ; seemingly attached along the upper edge of this process is a small unchitinised membrane covered with spicules. Laterally (fig. 10 *b*) the paraproct shows a small chitinised anterior area armed with stout bristles and situated below is a fine spiculate membrane which is rounded distally. Cercus narrow in ventral view and considerably wider dorsally than ventrally when seen from a lateral aspect. Unlike the bosses of the long bristles in the case of most species, those of *damnosum* are heavily pigmented.

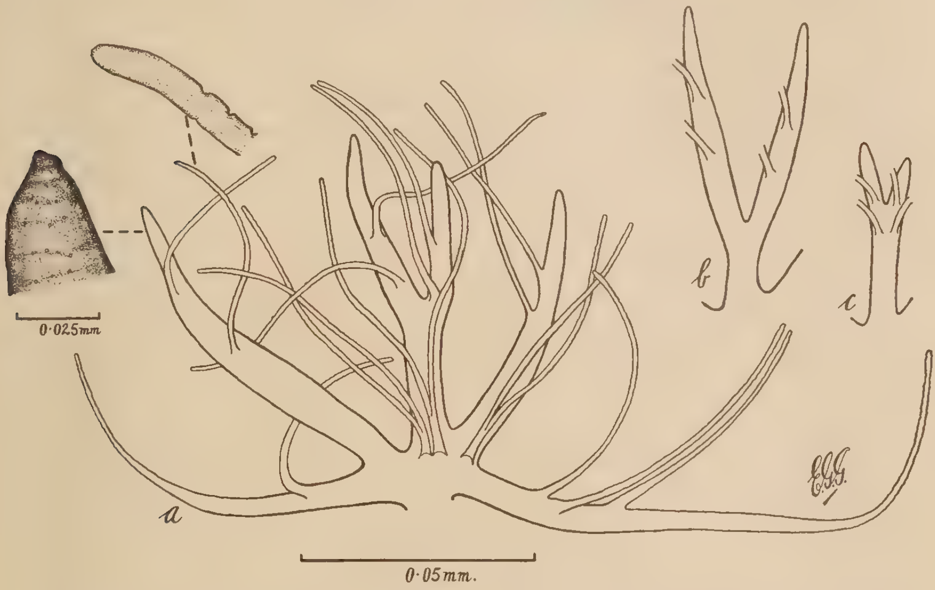

Fig. 11. *Simulium elgonensis* : *a*, ventral view of respiratory organ of pupa of Kabale specimen ; *b*, median bifid lobe of another example from Kabale ; *c*, median lobe of type form from Mt. Elgon drawn to the same scale.

Pupal Respiratory Organ of Simulium elgonensis, Gibbins.

S. elgonensis was originally described by the writer (1934) from a small number of specimens collected in the River Kaptokoi on Mt. Elgon in 1932. Subsequently further material of this species was obtained from the River Soroko near Budadari at the foot of the same mountain in November 1935. Critical examination of the respiratory organ has now shown that the example previously illustrated had lost one pair of its fragile slender secondary filaments from the base of the median bifid lobe. It should therefore have been correctly depicted with two pairs of slender filaments and not one pair near the base of the median lobe.

A large collection of *S. elgonensis* was received from Kabala in 1932 through the kindness of Mr. G. H. E. Hopkins. Many of these specimens had been isolated and their respective pupal pelts preserved. An examination of the pupal respiratory organ showed that the Kabale form was about twice the size of those from Mt. Elgon. In figure 11 the organ has been drawn from a Kabale specimen and an idea of the extent of variation of the median lobe in this district may be gained by comparison with fig. 11 *b*, which shows the lobe of another example. Drawn to the same scale, fig. 11 *c*, depicts the median bifid lobe of the type form from Mt. Elgon. The very much smaller size is apparent, and it will be seen that the two branches are short and the lower pair of secondary filaments arise from the main stem and not one from each branch as in the case of the Kabale form. The sculpture of the outer wall, though very similar in both cases, does not show so many pigmented nodules in the Kabale form. Isolated adults of both sexes of the Kabale form show no difference either in size, externally, or in the terminalia from those of the type form from Mt. Elgon.

Distribution of Simuliidae.

The specimens on which the distribution is based were determined by the writer mainly from those bred from isolated pupae but in a few cases from females caught in the act of biting and pupae which had not been reared.

Simulium adersi, Pomeroy.

Originally described by Pomeroy (1921) as a variety of *S. hirsutum* on the character of the respiratory organ of the pupa. Subsequently the present writer (1934) raised the insect to the status of a distinct species when the male, female, pupa, larva, cocoon and breeding-places were dealt with. Later (1936 *b*) further details were published of the male terminalia.

Distribution.—Entebbe district : Lake Victoria, Nkosi Island, 25.v.28 (*G. D. Hale Carpenter*) and Nsadzi Island, 8.viii.32 (*E. G. Gibbins.*)

Breeding-places.—Off the rocky shore of an island in Lake Victoria where the water is subjected to intense wave action, attached to clean smooth roots of trees lying in water varying in depth from six inches to three feet or more, depending on the waves. Pomeroy (1921) found the early stages on grass blades in a small stream in Zanzibar.

Blood-sucking habits.—Professor G. D. Hale Carpenter (1920) states that he was set upon in the early morning when on Kome Island, Lake Victoria, by a biting swarm of *S. adersi*. He notes that the species chiefly attacked the head, neck and ears. The present writer (1934) records their presence in large numbers in tsetse traps on Nsadzi Island. A survey of the population in contact with the fly showed no signs of onchocerciasis (Gibbins & Loewenthal, 1933).

Simulium africanum, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1934).

Distribution.—Bugishu district : Mt. Elgon, River Sipi, 7,000 ft., 3.v.32 and 8.v.32, River Kaptokoi, 6,000 ft., 4.v.32, and River Sasa, 9.v.32 (*E. G. Gibbins*).

Breeding-places.—Dashing mountain streams, on small loose alga-covered stones lying below cascades and attached to leaves and stems of an Umbellifer and a *Polygonum* growing above waterfalls.

Simulium brachium, Gibbins.

Male, female, pupa, larva, cocoon and breeding-places described by the present writer (1936 *b*).

Distribution.—Bugishu district : Mt. Nkokonjeru, River Naboinga, 6,000 ft., Bumboi, 28.iii.32 and River Nabigwo, 26.iii.32 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing streams, attached to stems and blades of grass and fern leaves dipping in the water and on roots hanging in effervescent water below falls.

Simulium cervicornutum, Pomeroy.

Male and female described by Pomeroy (1920) ; both sexes redescribed by the writer (1936 *b*) when the larva, pupa, cocoon and breeding-places were also dealt with.

Distribution.—Bugishu district : Mt. Nkokonjeru, River Nabigwo, Bunkoko, 26.iii.32, 27.iii.32 and 16.iv.32 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing stream, attached to grasses dipping in the water and stones lying on the river-bed in both heavy and light shade.

Simulium damnosum, Theobald.

Female described by Theobald (1903) ; female redescribed and male, larva, pupa, cocoon, breeding-places and blood-sucking habits described by the present writer (1933). The male terminalia were illustrated in detail (1935) and the female terminalia have been dealt with in detail in the present study.

Gibbins & Loewenthal (1933) reported on the infectivity of the female fly near Jinja, and further notes on its range of flight were given by the senior author (1936 *b*).

Distribution.—Busoga district : Near Jinja, 1902 (*Cuthbert Christy-Austen*, 1909) ; Jinja, 19.iv.27 (*J. Bequaert*) ; Buwenda, 26.vi.33, Jinja, 4.iii.32 and 18.v.32 (*E. G. Gibbins*). Mengo district : Busana, 2.vii.33, Nagoge, 3.vii.33, Kampala, 26.1.35 (*E. G. Gibbins*). Toro district : Busongoro, xii.27 (*G. D. Hale Carpenter*) ; River Mubuku, near bridge, 10.xii.31 (*E. G. Gibbins*). Ankole district : River Ruizi (4,600 ft.), Mbarara, 2.viii.36 (*E. G. Gibbins*).

Breeding-places.—Rapids of large, swiftly flowing rivers, attached to long pendulous grasses dipping deeply into the most aerated parts and adhering to the surface of rocks where the water dashes at its greatest speed.

Blood-sucking habits.—A vicious human blood-sucking species which mainly attacks the lower parts of the body. It has been proved by dissection to be a carrier of *Onchocerca volvulus* in Uganda. The female fly travels long distances and at certain seasons has been found as far as 45 miles from its nearest known breeding-place.

Simulium debegene, De Meillon.

Male and female described by De Meillon (1934). Male and female terminalia, larva, pupa, cocoon and breeding-places described by the present writer (1937).

Distribution.—Toro district : Mt. Ruwenzori, River Namwamba, Kyanjoke, 26.xii.34 (*E. G. Gibbins*).

Breeding-places.—Heavily shaded, swiftly flowing mountain river, attached to stones lying beneath cascades.

Simulium dentulosum, Roubaud.

Female described by Roubaud (1915) ; female redescribed and male, larva, pupa, cocoon and breeding-places described by the present writer (1934).

Distribution.—Bugishu district : Mt. Elgon, River Soroko, 3,600 ft. (*S. A. Neave*) ; River Sasa, 9,500 ft., above Bulambuli, 6.v.32, River Sipi, 7,000 ft., 3.v.32 and 6.v.32, River Cheptui, 6,000 ft., 4.v.32, River Kyebonet, 6,000 ft., 4.v.32 (*E. G. Gibbins*) ; Mt. Nkokonjeru, River Nabigwo, 6,000 ft., Lule, 1.iv.32, River Naboinga, 6,000 ft., Bumboi, 3.iv.32, River Kyagodo, 6,000 ft., 11.iv.32 (*E. G. Gibbins*).

Breeding-places.—Rapidly flowing mountain streams, attached to the fine roots of tree heath, threads of an alga-like plant, bright green juicy stalks and leaves of a species of Umbellifer in cascades and the swaying stems and leaves of a *Polygonum* growing in water three inches deep where it gathers momentum before falling into an abyss below.

Blood-sucking habits.—The type female was taken as an adult, but no details as to the circumstances of capture are available.

Simulium duodecimum, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1936 *b*).

Distribution.—Mengo district : River Kigwe, Bukalasa, 30.vi.32 (*E. G. Gibbins*) ; Masaka district : Masaka, 28.viii.32 (*G. H. E. Hopkins*).

Breeding-places.—Slowly flowing, lightly shaded streams, on dirty stones lying on the river-bed in muddy water eighteen inches deep and on the dirty stems and blades of grass dipping in the water.

Simulium edwardsi, Gibbins.

Male, female, pupa, cocoon and breeding-places described by the present writer (1937).

Distribution.—Toro district : Mt. Ruwenzori, River Namwamba, Kyanjoke, 6,500 ft., 26.xii.34, River Mpanga, Bwamba Pass, 17.xi.31 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing streams, attached to slender tree-roots and small stones present in cascades.

Simulium elgonensis, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1934). In the present study a slight variation in the pupal respiratory organ is figured.

Distribution.—Bugishu district : Mt. Elgon, River Kaptokoi, 5,000 ft., 5.v.32, and River Soroko, Budadari, 21.xi.35 (*E. G. Gibbins*). Kigezi district : Kabale, 6,000 ft., 26.x.32 (*G. H. E. Hopkins*). Ankole district : River Ruizi, 4,600 ft. Mbarara, 2.viii.36 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing mountain streams, attached to the leaves and stems of an Umbellifer and a species of *Polygonum* growing at the edge above a precipitous waterfall and on the surface of small alga-covered stones lying in the turbulent waters below rapids.

Simulium griseicolle, Becker.

Female described by Becker in 1903 ; female redescribed and male, larva, pupa and cocoon described by the present writer (1935 *a*).

Distribution.—Mengo district : Busana, 19.x.33 (*T. W. Chorley*).

Breeding-places.—Swiftly flowing large rivers, attached to rocks and plants growing at the water's edge.

Blood-sucking habits.—The two female specimens taken in Uganda were obtained from a guinea-fowl and were found to be engorged with blood. King (1908) states that the insect causes intense annoyance to human beings in the Sudan by its habit of crawling into the eyes, ears and nose and by continually pricking the skin in its ineffectual efforts to obtain blood. On a donkey he observed the fly to feed greedily and fly away with its abdomen enormously distended.

Simulium hargreavesi, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1934) who dealt with the male terminalia in greater detail (1935 *b*).

Distribution.—Busoga district : River Nile, 3,800 ft., 1924 (*H. Hargreaves*) ; River Nile, numerous places between Ripon Falls and Kimaka, 23.ii.32, 25.ii.32 and 4.iii.32 (*E. G. Gibbins*) ; River Nile, rapid above Owen Falls, 1.vi.36 (*A. M. Evans, E. G. Gibbins*).

Breeding-places.—Sunlit waters of a large swiftly flowing river, attached to the upright stems of reeds growing at the edge in the wash of the falls, on stalks and leaves of long filamentous grasses swirling in eddies, and on the clean, smooth tops of isolated rocks situated in mid-river. In rapids the early stages were particularly numerous and were found on rocks and grasses hanging from the bank.

Simulium hirsutum, Pomeroy.

Pomeroy (1921) described the male and female ; both sexes were redescribed by the present writer (1936 *b*), when descriptions of the larva, pupa, cocoon and breeding-places were also given.

Distribution.—Bugishu district : Mt. Nkokonjeru, River Nabigwo, 4,000 ft., near Bunkoko, 27.iii.32 and 16.iv.32 (*E. G. Gibbins*) ; Mt. Elgon, River Sipi, 6,000 ft., near Sipi rest camp, 1.vi.32 (*E. G. Gibbins*) ; Mengo district : River Sezibwa, 3,800 ft., near falls, 8.vi.32 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing streams, in heavy and light shade, on loose stones, both rough and smooth, lying beneath and above cascades and on elephant grass dipping in the water.

Simulium kauntzeum, Gibbins.

Male, female, larva, pupa and cocoon described by the present writer (1937).

Distribution.—Toro district : Mt. Ruwenzori, River Namwamba, Kiriruma, 10,200 ft., 25.xiii.34 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing partly shaded mountain river on the surface of clean dark stones lying below cascades in the river.

Simulium lepidum, De Meillon.

Male and female described by De Meillon (1935). Male and female terminalia redescribed and larva, pupa, cocoon and breeding-places described by the present writer (1937).

Distribution.—Toro district : River Mubuku, near Bridge, 21.xii.31 (*E. G. Gibbins*). River Namwamba, Kilembe, xii.34 (*F. W. Edwards*). Bugishu district : Mt. Nkokonjeru, River Nabigwo, 6,000 ft., Bumboi, 27.iii.32, foot of Mt. Elgon, River Soroko, Budadari, 30.xi.35 (*E. G. Gibbins*). Chua district : Agoro Mts., 20.xii.32 (*G. L. R. Hancock*). Ankole district : River Ruizi, 4,600 ft., Mbarara, 2.viii.26 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing mountain rivers, attached to the face of vertical rocks in falls and on blades of elephant grass dipping in rapidly flowing water.

Simulium masabae, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1934).

Distribution.—Bugishu district : Mt. Elgon, River Sipi, 7,000 ft., 3.v.32 and River Sasa, 9,500ft., above Balambuli, 6.v.32 (*E. G. Gibbins*) ; Mt. Nkokonjeru, River Nabigwo, 6,300 ft., Lule, 1.iv.32 and River Kyagodo, 6,000 ft., 11.iv.32 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing mountain streams attached to tree-roots and stalks and leaves of an Umbellifer present in cascades and on the stems and leaves of a *Polygonum* growing in shallow water.

Simulium neavei, Roubaud.

Synonym : *Simulium nyasalandicum,* De Meillon.*

Female first described by Roubaud (1915) ; redescribed in the present study.

Distribution.—Ankole district : West Ankole, 4,000–5,000 ft. (*S. A. Neave*). Toro district : Kijura, 5,000 ft., near Fort Portal, 16.x.31 (*E. G. Gibbins*).

Blood-sucking habits.—A human blood-sucking species. Dry (1922) associated the fly with a skin disease prevalent amongst natives in Kenya, and Hissette (1932) proved *S. neavei* to be a carrier of *Onchocerca volvulus* in the Belgian Congo.

Simulium nili, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1934) who gave further details of the male terminalia (1935 *b*).

Distribution.—Busoga district : River Nile, 3,800 ft., Jinja, near bridge, 27.ii.32, 4.iii.32, and 28.iii.32 (*E. G. Gibbins*) ; River Nile, rapid above Owen Falls, Jinja, 1.vi.36 (*A. M. Evans, E. G. Gibbins*).

Breeding-places.—Swiftly flowing large river, on the vertical side of slimy rock over which the water dashed at great speed, and occasionally on the blades and stems of long grass hanging in rapids.

Simulium obscurum, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places dealt with in the present study.

Distribution.—Bugishu district : Mt. Nkokonjeru, River Kisiwaki, Bufumbo, 13.iv.32 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing heavily shaded mountain stream, attached to stones present in small cascades. In one situation the early stages were obtained in almost total darkness in a rock cavern.

Simulium octospicae, Gibbins.

Male, female, pupa, cocoon and breeding-places dealt with in the present study.

Distribution.—Bugishu district : Mt. Nkokonjeru, River Naboinga, 6,000 ft., Bumboi, 3.iv.32 and River Kyagodo, 11.iv.32 (*E. G. Gibbins*).

Breeding-places.—Shaded mountain rivers, attached to fine tree roots hanging in waterfalls.

Simulium rotundum, Gibbins.

Male, female, pupa, cocoon and breeding-places described by the present writer (1936 *b*).

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* Through the kindness of Dr. F. W. Edwards the writer has been able to examine one of the five females on which Dr. De Meillon based his description of *S. nyasalandicum* (1930). The specimen which was labelled Mt. Mlanje, Nyasaland, 11.ix.1913 (*S. A. Neave*), proved to be identical with *Simulium neavei.*

Distribution.—Bugishu district : Mt. Elgon, River Kyebonet, 6,000 ft., 4.v.32 (*E. G. Gibbins*).

Breeding-places.—Heavily shaded, swiftly flowing stream, attached to leaves dipping in the water.

Simulium ruficorne, Macquart.

Synonyms : *S. beckeri*, Roubaud ; *S. diversipes*, Edwards ; *S. divergens*, Pomeroy.

Male and female redescribed and larva, pupa, cocoon and breeding-places described by the present writer (1936 *b*).

Distribution.—Bugishu district : Foot of Mt. Elgon, River Tabogonye, 4,000 ft., 8.v.32 (*E. G. Gibbins*). Mengo district : River Kitante, 3,800 ft., Kampala, 29.i.35 (*T. W. Chorley*).

Breeding-places.—Slowly flowing and usually muddy streams, on dead and living grass blades and stalks lying in a few inches of water exposed to bright sunlight.

Simulium ruwenzoriensis, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1934). The pupal respiratory organ of this species is variable ; the three different forms found in Uganda were described and figured by the present writer (1937).

Distribution.—Toro district : Foothills of Mt. Ruwenzori, River Mpanga, 5,000–7,000 ft., Bwamba Pass, 30.ix.31, 6.i.32, 25.1.32 (*E. G. Gibbins*) ; Mitandi, 20.ii.32 (*E. G. Gibbins*) ; River Namwamba, Kilembe, 4,500 ft., 3.xii.34 ; Kiriruma, 10,200 ft., 25.xii.34, and Kyanjoke, 6,500 ft., 26.xii.34 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing shaded mountain rivers, below cascades, attached to clean loose stones lying on the river-bed in water about one foot deep and also on slender tree-roots dipping in the water from the edge of the stream.

Blood-sucking habits.—Two females were caught at Mitandi, 6,000 ft., Toro, in February 1932. They were not observed to bite but were most annoying owing to their habit of flying round the head, alighting on the face and crawling into the eyes. The species was particularly troublesome on the plains below Kilembe in Busongoro in December 1934. As on the previous occasion, they were not found to bite but swarmed round the head in large numbers getting into the hair and eyes.

Simulium simplex, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1936 *b*).

Distribution.—Bugishu district : Mt. Nkokonjeru, River Kyagodo, 11.iv.32, and River Naboinga, 6,000 ft., Bumboi, 13.iv.32 and 18.iv.32 (*E. G. Gibbins*) ; Mt. Elgon, River Kaptokoi, 5,000 ft., 4.v.32, and River Cheptui, 4.v.32 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing mountain streams on blades and stems of grass, fern leaves and tree-roots dipping in waterfalls.

Simulium taylori, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1937).

Distribution.—Toro district : Foothills of Mt. Ruwenzori, River Mpanga, Bwamba Pass, 17.xi.31 (*E. G. Gibbins*).

Breeding-places.—Dashing mountain stream, heavily shaded, attached to clean stones removed from the water below cascades.

Simulium tentaculum, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1936 *b*).

Distribution.—Bugishu district : Mt. Nkokonjeru, River Naboinga, 6,000 ft., Bumboi, 28.iii.32, and River Nabigwo, 6,000 ft., Lule, 1.iv.32 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing streams, on small black stones peppered with round holes lying a few inches below the surface of the water. The larva chooses one of the small holes, pupates and makes a cocoon which completely covers it.

Simulium touffeum, Gibbins.

Male, female, pupa, cocoon and breeding-places described in the present study.

Distribution.—Bugishu district : Mt. Elgon, River Sipi, 6,000 ft., near Rest Camp, 1.v.32, River Kaptokoi, 6,000 ft., Sabei, 4.v.32, and River Soroko, Budadari, 20.xi.35 (*E. G. Gibbins*).

Breeding-places.—Swiftly flowing shaded rivers, on clean and dirty stones lying beneath small cascades.

Simulium ugandae, Gibbins.

Male, female, larva, pupa, cocoon and breeding-places described by the present writer (1934).

Distribution.—Bugishu district : Mt. Elgon, River Abutakwe, 6,000 ft., near Sabei, 5.v.32 (*E. G. Gibbins*).

Breeding-places.—Heavily shaded stream, on loose stones, both clean and dirty, lying on the river bed below small cascades, and on leaves and stalks of a *Polygonum* dangling in the water.

Simulium unicornutum, Pomeroy.

Pomeroy (1920) first described the species on the character of the respiratory organ of the pupa ; subsequently (1921) he described the male and female, which were redescribed by the present writer (1936 *b*) when the larva, pupa, cocoon and breeding-places were also dealt with.

Distribution.—Mengo district : River Sezibwa, Kampala-Jinja Road, 7.ii.32 (*E. G. Gibbins*).

Breeding-places.—Slowly flowing shaded stream where no visible aeration was perceptible, attached to the leaves of a *Potamogeton* growing in shallow water and also on the upright stems of growing papyrus and on grass blades dipping in the stream.

Simulium violaceum, Pomeroy.

Described by Pomeroy (1921) as a variety of *S. alcocki* on the character of the respiratory organ of the pupa ; raised to the status of a species by the present writer (1936 *a*) when the male and female terminalia were described.

Distribution.—Masaka district : Masaka, 28.vii.32 (*G. H. E. Hopkins*).

Breeding-places.—Fast-flowing streams attached to small stones.

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NOTES ON THE LIFE-HISTORY OF *ERIOPHYES CARINATUS*, GREEN.

By C. B. Redman King.

(*From the Tea Research Institute of Ceylon.*)

Eriophyes carinatus, Green, is commonly known as " Purple Mite " in Ceylon. It was first described by Green[1] under the name of *Typhlodromus carinatus*, the generic name subsequently becoming *Phytoptus*, and finally (up to the present time) *Eriophyes*.

Besides Ceylon, the mite is also found in North India and Java, and the only food-plant recorded is tea. In status it is one of the lesser pests of tea, although in times of drought some defoliation may follow its attack. Badly affected leaves turn a bronze colour, and both surfaces may be seen to be dusted with fine white specks, betraying the cause ; these specks being the cast skins of the mites.

Eriophyes carinatus appears sometimes to favour the upper parts of a leaf, but this may be due, at least in part, to a preference for smooth surfaces, for when the lower surface shows hairiness, fewer are to be found here ; but where it is devoid of hairs the mite is not markedly less numerous than it is above.

Life-History.

It seems that up to the present time the eggs of Purple Mite have evaded recognition. An acute observer, E. E. Green[1], could only state, in 1890, " Although colonies contain every age and size, I have been unable to find anything resembling the eggs of this species." In 1895, the mite was found doing considerable damage in parts of Assam, and concerning the egg stage, Watt[2] writes as follows :— " Certain leaves seem to be specially set apart for the purpose of breeding. On the under surface of these leaves will be found numerous thickened patches like little warts. On looking through the leaf, these are seen as transparent, pale-coloured spots . . . . . On careful examination they will be found to be cavernous formations within the tissue, just below the epidermis, and contain what I take to be the eggs of the Purple Mite. Apparently the mites on escaping from these blisters or wart-like houses wander off to other leaves to feed ; and it would seem that on moulting they conjugate under the shelter of the veins on the upper surface. . . . . . I never came across, though I looked carefully over many samples, a warted or blistered leaf bearing also the powdery deposit of cast off skins." The only other observation on this matter that has been found is by Light[3] in 1927, who says :—" The eggs have not so far been recorded, and it is thought that the mite may be parthenogenetic." It seems probable that " viviparous " was intended for the word " parthenogenetic."

As may be surmised from the above, the eggs are not easy to find. They have now, however, been discovered, and it will be seen that Watt's conjectures have not been substantiated.

According to Banks, the eggs of gall-forming Eriophyidae are almost spherical. The eggs of the Purple Mite, however, are minute and circular, some 70–80μ in diameter, and about 10–11μ thick at the centre, the general shape being somewhat that of a watch glass with the rim touching the surface. They are colourless and almost transparent, and under magnification appear as green as the surrounding leaf tissues. It is no doubt this which has rendered them so difficult to find. Although they may just be detected by a powerful hand-lens as minute, green blisters, they may easily be passed over if the observer be uncertain what he is expecting to find.

The photomicrographs show a much greater differentiation from the surrounding surface than appears to the naked eye.

When first laid, the chorion has a somewhat wavy pattern, as judged by reflected light, but after about two days the skin appears to tighten up, giving an almost smooth surface, but a faint sculpturing may be detected. No further change is noticeable until a short time before hatching, when a slight mauve tint may be visible. Hatching takes place about 6–7 days after oviposition, at a temperature of about 72°F.

Larva.—After hatching, the larva appears as a naked, shiny, narrowly pear-shaped body, in colour a pale amethyst. The abdominal skin exhibits fine transverse striations, which are present in all subsequent stages. The first moult takes place after about one day.

Although Banks[4] states that in the ERIOPHYIDAE there is but one nymphal stage, in the case of *Eriophyes carinatus* there are certainly two.

First Nymphal Stage.—This stage at first resembles the larva, although slightly larger, but in a few hours the waxy ridges characteristic of this mite have made their appearance. The height of these ridges at their maximum, which is the same at each subsequent stage, is $10–11\mu$. In thickness they are about 1μ.

Second Nymphal Stage.—After the second moult, the ridges again appear, about 4μ thick, but they look broken and ragged.

Adult.—After the third moult the adult stage is reached, characterised by the appearance, after a short time, of the ridges, which are now of maximum size, about 11μ both in height and width, and continuous, although in old individuals they may look broken and ragged. The ridges described are confined, in all the stages in which they appear, to the abdominal region, and number five, one running along the middle of the dorsum, one along each side, and one each half-way between these and the dorsal ridge. The anterior ends of the three middle ridges are joined by a very thin projection, of about the same height, and from each side of the centre, about half-way to the middle ridges, two similar waxy outgrowths pursue a deviating course forwards, enclosing what Green[1] calls an " hour-glass " shaped space. The forward ends join a sort of waxy cap above the region of the beak. The lateral abdominal ridges also have a prolongation, similar in appearance to the others, but double, and follow the contour of the side of the body, separating near the cap and forming in plan a narrow loop. The cephalothoracic ridges are therefore distinguished from those of the abdominal region by being very thin and have the appearance of a hyaline ribbon standing on edge.

At each moult, the waxy ridges are shed with the skin, and the newly emerged mite shows a shiny and continuous surface, but the transverse striations are interrupted along the lines where the wax will be secreted.

The colour has slightly deepened and after the mites die becomes deeper still, showing a strong purple.

Like other members of the same family, the mites at all stages are provided with only two pairs of legs with which they drag themselves about, trailing the abdomen behind. The posterior end of the abdomen is provided ventrally with a sucker, which enables the mite to erect itself perpendicularly in the air, which position it may keep for some considerable time. The purpose of this manoeuvre is not as yet understood.

Sexes.—The sexes are distinguished by relative size. Although the cephalothorax is of about the same size in both sexes, the abdomen of the female is about twice as long as that of the male. Linear measurements of the cephalothorax in the feeding position gives values of $45–50\mu$ in both sexes, whereas the abdomen in the female varies between 103 and 126μ, the corresponding figure for the male being $55–60\mu$.

The sexes may also be distinguished by the method of feeding. The female while taking in nourishment stays quite still, but the male is restless and "marks time" with its feet without cessation, often very slowly changing its situation the while.

Up to the present time, neither copulation nor oviposition has been observed.

The life-cycle may be set forth as follows :—

	1. No. of individuals	2. No. of days	4. Temperature		3. Average days
			Max.	Min.	
Egg incubation	15	5	77·7	66·3	6
	41	6	77·7	66·3	
	13	7	77·7	66·3	
	2	8	77·7	66·3	
	6	6	80·0	66·0	6
	4	6	80·6	66·3	6
Larva	47	1	77·0	66·0	1
	1	2	77·0	66·0	
	6	1	80·0	66·0	1
	4	1	80·6	66·3	1
1st nymphal stage	2	1	80·0	65·5	2·14
	15	2	80·0	65·5	
	5	3	80·0	65·5	
	4	3	80·0	66·0	A 2·7
	2	2	80·0	66·0	
	3	1	80·6	66·3	1·25
	1	2	80·6	66·3	
2nd nymphal stage ...	5	1	80·5	63·5	D 1·7
	11	2	80·5	63·5	
	6	2	80·0	66·0	F 2
	3	2	80·6	66·3	B 1·75
	1	1	80·6	66·3	
Total cycle	2	11	80·0	66·0	11·7
	4	12	80·0	66·0	
	4	10	80·6	66·3	10
Pre-oviposition period ...	3	2	80·3	65·6	2
	1	1	80·3	65·6	

The maximum number of eggs laid by a female, so far observed, is 13, the rate usually being one per diem, but occasionally two may be laid on the same day. Oviposition, once started, is continuous, and there may be a lengthy period afterwards in which there is no further oviposition.

Purple Mite females, segregated from the time of hatching, lay eggs which invariably develop into males.

Control.

In recent times, this mite has not been sufficiently troublesome to demand any artificial contra-measures. If it ever does so, a light application of fine sulphur dust, suitably applied, would be enough to check it. As it is, conditions generally seem to be enough to prevent it from becoming as dangerous as either the Yellow Mite (*Tarsonemus translucens*, Green) or Red Spider (*Tetranychus bioculatus*, Wood-Mason).

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NOTES ON TWO NEW ORIENTAL PARASITES OF THE COFFEE MEALY-BUG (*PSEUDOCOCCUS LILACINUS*).

By Ch. Ferrière, D.Sc.

In connection with his biological researches for the control of the coffee mealy-bugs in Africa, Mr. R. H. Le Pelley recently made a trip to the Far East in order to try to find some Oriental parasites of *Pseudococcus lilacinus* which could be introduced into Kenya Colony.

In the Philippine Islands he was able to breed two species, both belonging to the Encyrtidae. One, specially important, a new species of the genus *Pseudaphycus*, Clausen, has been sent for acclimatisation to Kenya; the other, an *Anagyrus*, Howard, belonging to a group most species of which attack mealy-bugs in different countries, proved to be also a new species. The types of the two species described here are deposited in the British Museum.

Pseudaphycus orientalis, sp. nov.

♀♂. Head orange-yellow, the cheeks and mouth pale yellow, almost white, the ocelli and tip of mandibles reddish brown, the eyes black. Thorax with the mesonotum, axillae and scutellum orange-yellow, the scutellum with a brown transverse stripe behind the middle; posterior margin of pronotum, the tegulae and the lower part of the thorax whitish; anterior part of pronotum and the propodeon brownish. Abdomen yellowish with transverse brown stripes, and the tip of the ovipositor broadly brown. Antennae with the scape yellow below, brown above, the pedicel and funicle more or less brown, the 5th joint (except a line below) and the club white. Legs whitish, the middle and hind tibiae with two brown annelli more or less well marked, the tarsi yellowish. Wings with a faint dusky cloud below the stigmal vein beyond the oblique hairless streak.

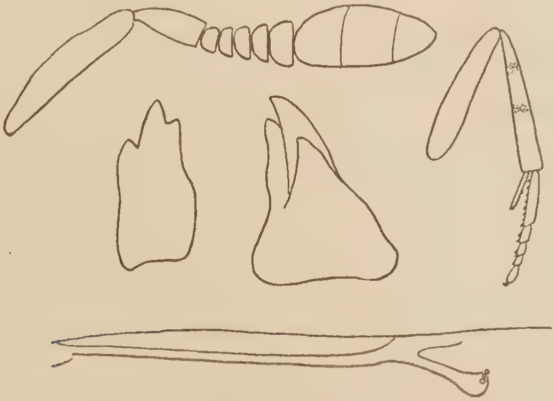

Fig. 1. *Pseudaphycus orientalis*, sp. n. ♀: antenna, mandible from the side and from below, middle leg and wing nervature.

♀. Head rounded in front, the face inflexed; fronto-vertex shagreened, about twice as long as wide, the inner margin of the eyes parallel; ocelli forming an acute-angled triangle, the hind ocelli half as far from each other as from the front ocellus and close to the eye margin. Mandibles with three teeth, the middle one the longest, curved, the upper tooth distinctly shorter and the lower tooth the shortest. Antennae inserted at the base of the face near the sides of the clypeus ; scape slightly broadened, reaching little above the antennal furrows ; pedicel narrow, a little more than twice as long as wide and as long as the first four funicle joints united ; funicle with 5 joints, the 1st rounded, the following increasing in width, transverse, the 5th larger than the 4th ; club large, with 3 joints, longer than the funicle. Thorax finely shagreened, dull, covered with white ciliae ; mesonotum transverse, about two and a-half times as broad as long ; axillae triangular, meeting in the middle ; scutellum strongly narrowed behind ; propodeon very short in the middle, where it is hidden below the tip of the scutellum, broadened on the sides. Wings normal ; marginal vein punctiform, stigmal vein rounded at tip and about twice as long as the postmarginal. Wings closely ciliated ; the oblique hairless streak interrupted below the middle and not quite reaching the posterior margin of the wing. Legs normal, the metatarsi as long as the following tarsal joints together. Abdomen triangular, shorter than the thorax. Ovipositor protruding by about 1/5 of the length of the abdomen.

♂. Similar, slightly smaller, the antennae with the pedicel narrower, the funicle joints shorter and more transverse, the 5 joints together scarcely longer than the pedicel ; club not divided, large, almost twice as long as the funicle.

Length : ♀♂, 0·50–0·75 mm.

Philippine Is. : Los Baños, ix.1936.

Described from 8♀ and 4♂ mounted dry and 28♀ and 9♂ in microscopical preparations.

This is the first species of *Pseudaphycus* found in the Oriental region. Of the other seven known species, four are from the United States, one has been bred in Mexico and introduced into Hawaii, and two have been found in Europe. All are parasites in Dactylopiinae, mainly *Pseudococcus* spp.

We have compared the descriptions of all these species and have drawn from them, with the aid of a small key of American species given by Timberlake (1916), a table of all the known species, from which the position of the new Oriental species will best be seen.

1.—Wings entirely hyaline..........2

Wings more or less (sometimes only slightly) infuscated..........3

2.—Face and cheeks normal. Coloration bright yellow. Pubescence of mesonotum dark. Size 1·08–1·44 mm..........*utilis*, Timb.

Face and cheeks shortened. Coloration pale yellow. Pubescence of mesonotum white. Size 0·6–0·9 mm..........*graminicola*, Timb.

3.—Ovipositor barely protruding. Fifth funicle joint and club white.......... *prosopidis*, Timb.

Ovipositor protruding at least 1/5 the length of the abdomen..........4

4.—Wings with two distinct transverse clouds, widely separated.......... *maculipennis*, Mercet

Wings with a faint brownish cloud beyond the oblique hairless streak, sometimes interrupted by a narrow hyaline line..........5

5.—Fronto-vertex as long as wide ; ocelli in an equilateral triangle.......... *austriacus*, Mercet

Fronto-vertex two or three times as long as wide ; ocelli in an acute-angled triangle..........6

6.—Oblique hairless streak of forewings not interrupted..............*websteri*, Timb.

Oblique hairless streak interrupted a little beyond middle and not quite reaching the posterior margin of wing..7

7.—Fronto-vertex nearly three times as long as wide, the dorsal orbits of eyes diverging anteriorly. Pedicel little longer than the first three funicle joints combined...*angelicus*, Howard

Fronto-vertex only twice as long as wide, the dorsal orbits of eyes parallel. Pedicel as long as the first four funicle joints combined......*orientalis*, sp. n,

The genus *Pseudaphycus*, Clausen, is very closely related to the genus *Acerophagus*, Smith. Timberlake (1916) in his key to the genera separates them only by the form of the mandibles, thus :

> " 4.—Two upper teeth of mandibles nearly equal, lower tooth more basal and smaller ....*Acerophagus* Smith
>
> Upper and lower teeth of mandibles equal, middle tooth larger and very sharp ....*Pseudaphycus* Clausen."

Judging only by this character, the species described here should come under *Acerophagus*, especially as Timberlake has drawn figures of mandibles of this genus in which the middle tooth is larger than the upper tooth. In his description of *Acerophagus debilis*, Timb. 1924, from Hawaii, he says : " Mandibles of the usual type, with the outer tooth far basad and the middle tooth considerably larger than the inner tooth." This does not agree with the character given in the key, and his drawing is very much the same as our figure of the mandible of *Pseudaphycus orientalis*. This last species is, however, certainly a *Pseudaphycus*, more closely related to *P. angelicus*, How., than to any other species.

After comparison of the generic characters given by Timberlake and of the description of all the species of both genera, we believe that these genera can best be distinguished by the following characters :

Fronto-vertex generally broad, as long as wide or at least less than twice as long as wide, the ocelli more frequently arranged in a right or obtuse-angled triangle. Body entirely yellow, antennae and legs more or less concolorous, the club not white..*Acerophagus*, Smith

Fronto-vertex generally narrower, twice (or more) as long as wide, the ocelli in an equilateral or acute-angled triangle. Body yellow or orange, more or less dusky, the underside paler yellow ; antennae more or less brownish, the club whitish...*Pseudaphycus*, Claus.

Anagyrus lilacini, sp. nov.

♀. Head orange, slightly darkened at the base of the cheeks, occiput black except at sides. Thorax black above, slightly reddish on the sides of pro- and mesonotum and near the tip of the scutellum ; mesopleurae entirely orange-yellow, propleurae whitish ; tegulae white. Abdomen black. Antennae pale orange-yellow, the club more white ; scape black with an oblique yellow stripe before the tip, pedicel black at base, yellow at tip, 1st funicle joint black except at apex. Legs whitish, with black lines or spots at end of femora and at base of tibiae ; tarsi orange-yellow. Wings hyaline.

Head dull, finely granulated, face and cheeks covered with short white ciliae ; eyes large, converging slightly above, finely and densely ciliate ; fronto-vertex about 1·5 times as long as wide in the middle, ocelli in an obtuse-angled triangle, the posterior ocelli as far from the eye margin and from the hind margin of head as their own diameter. Cheeks short, about as long as half the breadth of an eye. Antennae inserted near the mouth ; scape moderately broad, a little more than twice as long as broad ; pedicel slightly more than twice as long as broad ; 1st funicle joint as long as the pedicel, but narrower, the following joints slightly shorter, the 6th still almost twice as long as broad ; club narrow, longer than the two preceding joints together. Thorax normal, not depressed. Mesonotum and scutellum dull, finely punctate, densely covered by a short white pubescence ; mesonotum about twice as broad as long ; scutellum triangular, its apex extending over the middle of the postscutellum and reaching the base of the propodeon. Axillae meeting in the middle. Propodeon narrow in the middle, broader on the sides, the spiracles small and rounded. Wings moderately broad, reaching beyond the end of the abdomen ; marginal vein very short, not or scarcely longer than broad ; postmarginal vein absent ; stigmal vein narrow, only slightly broadened apically and almost three times as long as the marginal. Disk of wing entirely covered with short ciliae, except for the oblique hairless line, which is broadly interrupted below the middle. Abdomen triangular, as long as head and thorax together, compressed and pointed at apex. Ovipositor scarcely or very slightly protruding, the sheaths compressed. Hypopygium reaching a little beyond the tip of the last tergite.

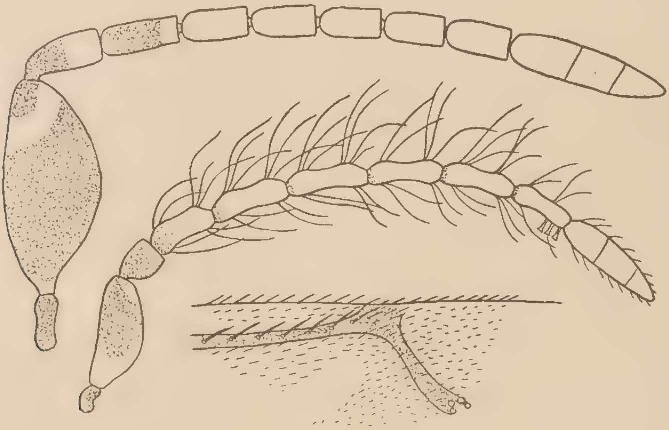

Fig. 2. *Anagyrus lilacini*, sp. n. : antennae of female and male ; wing nervature.

♂. Body black, mandibles reddish, sides of pronotum whitish, anterior part of mesopleurae slightly orange. Antennae white, the scape with a broad black oblique stripe behind the middle, the pedicel black, the 1st funicle joint brown and the base of the other funicle joints with a small black spot.

Head, seen from in front, rounded or slightly longer than broad, fronto-vertex broader than long, the ocelli forming a right-angled triangle, the hind ocelli near the margin of the head. Antennae inserted near the mouth ; scape short, about twice as long as broad and as long as the pedicel and 1st funicle joint together ; pedicel not longer than broad ; 1st funicle joint about 1·5 times as long as the pedicel but narrower, all the other funicle joints sub-equal in length, except the last which is a little shorter ; each has two irregular whorls of long curved hairs ; club not quite as long as the two preceding joints together, with shorter hairs ; there is a row of three conidium-like setae near the end of the 6th funicle joint, but none at the base of the club. Thorax and abdomen smaller than in the female, the abdomen shorter than the thorax. Wings shorter and broader, the discal ciliation fine and white, not easily seen ; marginal vein punctiform, as long as broad ; postmarginal vein almost absent ; stigmal vein somewhat shorter and broader at apex than in female.

Length : ♀ 1·75 mm. ; ♂ 1 mm.

Philippine Is. : Los Baños, ix.1936.

Described from 5 ♀ and 3 ♂.

This species belongs to a group of *Anagyrus*-species which are closely related in the coloration of the body and antennae. It is with some reluctance that we add a new species to this group, several species of which may be only varieties or geographical races of a widely distributed species. But it differs sufficiently from all other known species to require a new name, and systematically, with our present knowledge, it is of no great importance if this form is considered a distinct species or a race.

It is specially related to *Anagyrus greeni*, Howard, from Ceylon and to *A. pseudococci*, Girault, from South Europe.

From *A. greeni*, Howard 1896, it differs in having the dorsum of the thorax blackish and the legs with dark spots and lines. Moreover the fronto-vertex is distinctly longer than broad, whereas Timberlake (1932) says for this species: "Fronto-vertex broader than long." Also the ovipositor is not "distinctly protruded."

From *A. pseudococci*, Girault 1915, of which we have examined specimens from Algeria, it differs specially by the relative length of the antennal joints. In *pseudococci* the scape is broader and larger, the pedicel about 1·5 times as long as the 1st funicle joint and the 6th joint is less than 1·5 times as long as broad. The vertex is also narrower and the thorax is more yellowish.

A. bohemani, Westwood, as redescribed by Mercet (1921), should also belong to this group. But according to Westwood the antennae are brown with only the last joint white, and an old specimen in the British Museum under that name agrees with Westwood's description. We believe therefore that the *bohemani* of Mercet is a synonym of *pseudococci*, Girault. The specimens received from Algeria, parasites of *Pseudococcus vitis*, agree as well with Mercet's description of *A. bohemani* from Spain as with Girault's description of *A. pseudococci* from Sicily.

Anagyrus saccharicola, Timberlake 1932, found in the Philippine Is. on *Trionymus sacchari*, Cock., differs by the strongly depressed form of the body of the female, the thorax being "scarcely one half as thick dorso-ventrally as the greatest width" and the apex of the four-sided scutellum being "not at all elevated above level of propodeum and fitting into a depression in the middle of the latter." Moreover the head and thorax are much more orange-yellow.

A. dactylopii, Howard, a parasite of *Pseudococcus filamentosus* in China, introduced into Hawaii, has, according to Timberlake (1932), the head and thorax almost entirely orange-yellow, the eyes almost bare (whereas in most other species they are distinctly and coarsely ciliated), the pedicel clearly longer than the 1st funicle joint and the postmarginal vein distinct, a little shorter than the marginal.

A. aurantifrons, Compere 1926, bred from *Pseudococcus* spp. in Africa, of which we have series of specimens obtained from the coffee mealybugs in Kenya, differs especially by the much broader scape, the longer pedicel, which is longer than the 1st funicle joint, the narrow funicle, the last joint of which is almost quadrate, and the longer marginal vein, which is about twice as long as broad.

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AN INDIAN CERAMBYCID DAMAGING TEA CASES.

By Fritz van Emden.

During November 1936, a fine powder was noticed dropping from tea cases on the premises of an industrial firm in London. These cases were constructed of three-ply wood which originated probably from Scandinavia; it had been brought to India and remained there for probably about 18 months. The cargo arrived in this country in March 1936 and had been lying untouched in the warehouse till November. The interior of the cases was lined with tin. When this was removed, large flat cavities containing living larvae were discovered. Samples were sent to the Imperial Institute of Entomology with a request for information if possible as to where infestation of the timber took place.

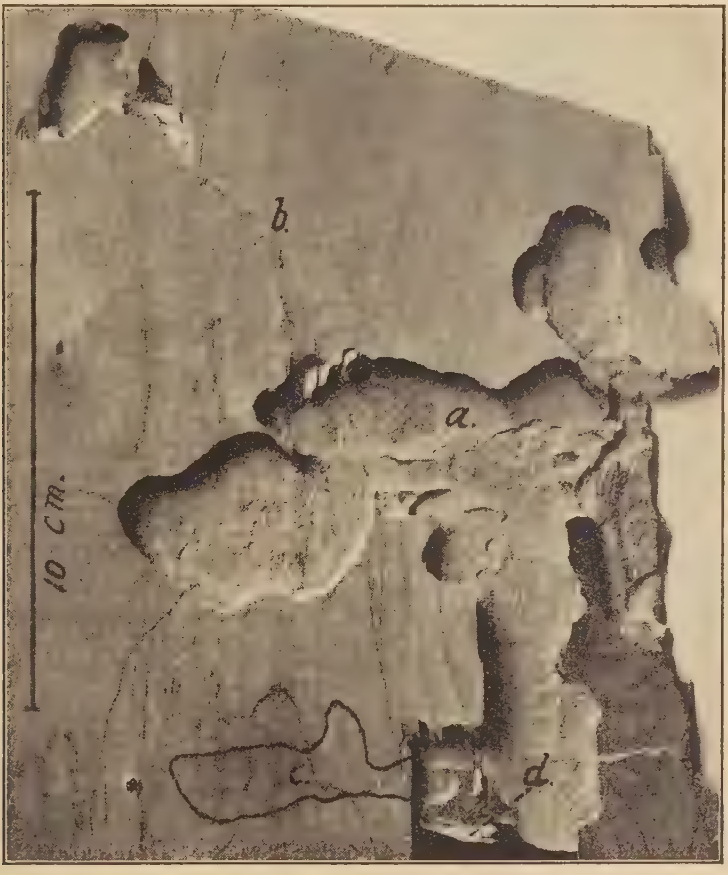

Fig. 1. Large cavities made by larvae of *Stromatium barbatum*, F.: *a*, striation produced by mandibles of the larva; *b*, *c*, galleries of larvae; *d*, frass.

There were no beetles, either dead or living, in the sample, but 6 living larvae. These proved to be CERAMBYCINAE, and have been identified as *Stromatium barbatum*, F. (for description of larva see Gardner, Indian Forest Records, Ent. Ser. **13,** pt. 2, 1927, p. 40, figs.). They do not agree with any known Scandinavian or British Cerambycid larvae, nor is there any genus in these countries in which larvae of such a size are known ; thus it is evident that the cases must have been attacked in India.

Stromatium barbatum is known as occurring from Madagascar to Burma and the Andaman Islands. It attacks practically all soft to hard sorts of dry wood and is doing considerable damage in India. Beeson lists a great number of woods which have been attacked by its larvae (Indian Forester **45,** 1919, p. 148).

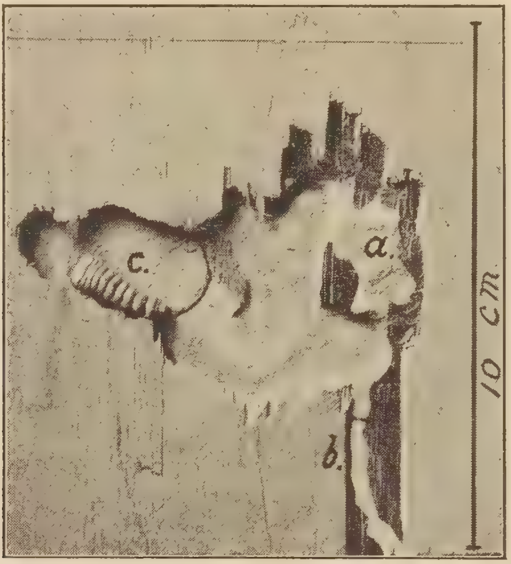

Fig. 2. Smaller gallery of larva of *Stromatium barbatum*, F. The part to the left of the black line is hollow and translucent, the rest filled up with frass : *a*, frass ; *b*, gallery of younger larva ; *c*, larva in its gallery.

As this species and the genus *Stromatium* have not yet been recorded as being found in Great Britain, this occurrence seems worth noting. Further interest lies in the fact that the damage is in three ply timber and would seem to indicate a change to some extent in the habits of the larva. For whereas *Stromatium fulvum*, Vill., produces long narrow galleries (as figured by Silantjev, Hor. Soc. Ent. Ross. **38,** 1907–08, p. 185–282), the damage to the tea cases is in the form of large, wide cavities, which are usually widely open beneath the tin and reach nearly the outer side of the wood, so that only a thin wall remains of the 4 mm. of thickness. This wall is nowhere perforated, so that the case is apparently intact, but in some places a very light pressure will suffice to crush the thin outer wall and expose the tin. Most of the galleries are less extensive than that shown in fig. 1. But the existence of several of the larvae together in any of the larger burrows has not been observed by the firm.

As with many other wood-boring insects the wall of the gallery shows a fine striation produced by the mandibles of the larva (see *a* in fig. 1 and fig. 25 of the paper of Silantjev). One can see that the larva always begins by eating a narrow gallery (*b* and *c* in fig. 1 ; the wood has been half broken at *b*, so that the course of the gallery is by chance very evident there), which is later enlarged. These galleries, as well as the older parts of the cavities, are filled up with densely packed frass (fig. 1 *d*, fig. 2 *a*). Younger larvae attack mainly the middle layer (fig. 2 *b*), so that the board seems to be sound on both sides, only a creaking sound then revealing the activities of the larva. But on holding such a board against the light, it is seen to be hollow in some places. The sound produced by the mandibles of the larva is very striking also with *Stromatium fulvum* (Reikhardt, Karakulin and Isachenko, Pests of timber and their control, Moscow 1930 ; see Rev. appl. Ent. A, **18**, 1930, p. 189). Of course the hollow parts seen against the light are only a minor part of the damage done, for the larvae do not eject their frass from the burrows, but pack it up tightly in the galleries and cavities. It is thus impossible to estimate the extent of the damage simply by examining the board against the light. In the piece shown in fig. 2 only the part (containing the larva) to the left of the black line, was seen to be hollow, the much more extensive area being filled up with frass appeared to be sound.

ECONOMIC INSECTS AND BIOLOGICAL CONTROL IN THE BRITISH SOLOMON ISLANDS.

By R. J. A. W. Lever, B.Sc., D.I.C., A.I.C.T.A., F.L.S.

(Map.)

A previous paper[1] in this Bulletin dealt with the economic entomology of the British Solomon Islands Protectorate up to the year 1932. The present article concerns research conducted after that date with special reference to the biological control of two insect pests.

Climate.

There is comparatively little seasonal variation except for the direction of the wind, which blows chiefly from the north-west (monsoon) from November till about March and from the south-east (trades) from March till October. The seasonal index, *i.e.*, the ratio of rain falling in the wettest as compared with the driest month, averages 4·6 over the last five years; this figure is nearly twice that for the New Hebrides[2] to the south-east of the Solomon Islands. The mean of the mean maximum and minimum shade temperature, rainfall and relative humidity are shown in fig. 1. If the mean monthly temperature as ordinate is plotted against the mean daily rainfall of each month as abscissa, so as to give a hythergraph (fig. 2), it will be

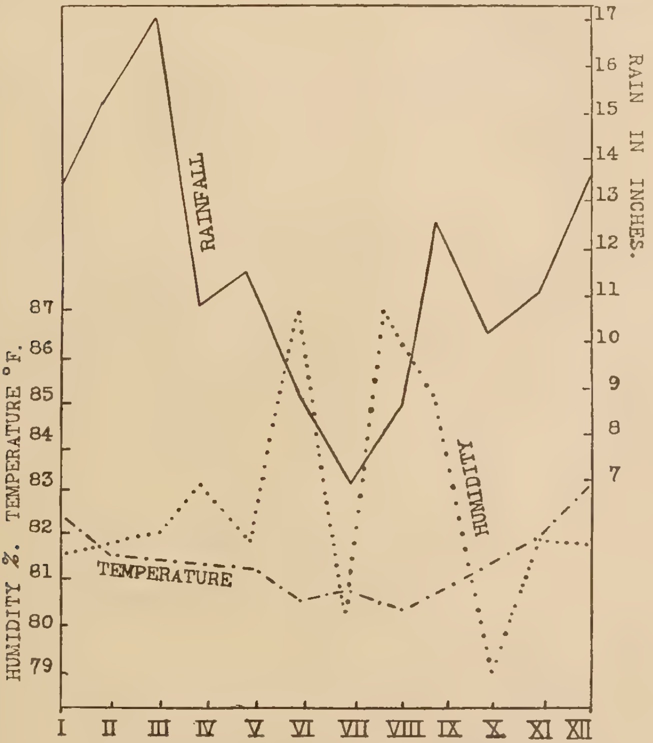

Fig. 1. Rainfall, humidity and temperature at Tulagi for 5 years.

seen that the wettest and hottest months (January to March) coincide, as do the driest and coolest (June to September). The above figures are for ten years in Tulagi, where alone full meteorological data are recorded. The large island of Guadalcanal to the south has a rainfall of only 70 inches in the middle of the northern coast, but one of 165 inches is found 50 miles further east on the same coast. The small Three Sisters, north of San Cristobal, average 190 inches, but this is exceeded on Vanikoro Island, Santa Cruz, with a mean of 225 inches.

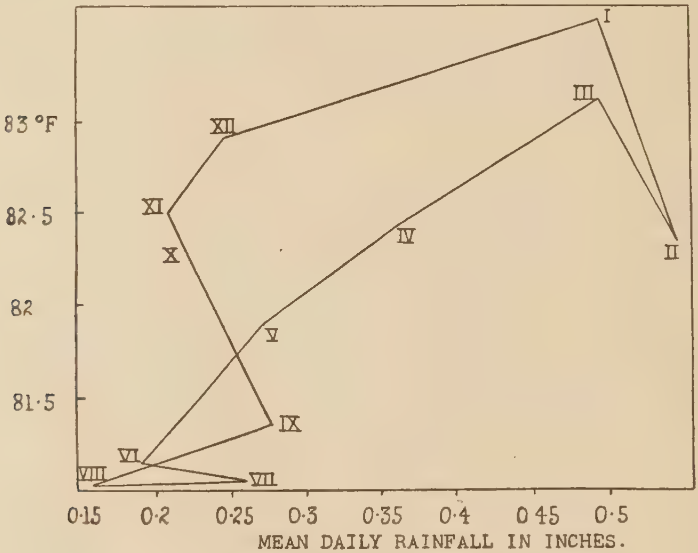

Fig. 2. Hythergraph: average for 10 years, Tulagi.

Topography.

The six large and many small islands which form the Protectorate are covered with dense jungle to their summits; the larger islands, which reach a length of over 100 miles, have considerable areas of "lateritic" soils derived from basalt or andesite. The small islands of Savo and Simbo and the larger islands of Vella and Guadalcanal have thermally active regions with sulphur springs and solfataras. The dry region on Guadalcanal has extensive grass-plains covered with two coarse grasses, *Imperata cylindrica* and *Themeda australis*. Lying 100 miles due south of Guadalcanal and separated from it by water nearly 3,000 fathoms in depth is Rennell (not shown on the map) which has a lake 10 miles long filling the former lagoon of this raised atoll. The only active volcano is the small island of Tinakula, north of Santa Cruz.

Ecological Areas.

The following are the major ecological areas as found in the 500 miles of the Protectorate and are seen to agree well with those of the New Hebrides to the south-east[3].

1.—Littoral: (*a*) coral, coral sand, small atolls and artificial islands of Malaita; (*b*) mangrove swamps; (*c*) shore flora.

2. Grass-plains of Guadalcanal.

3. Mountains: (*a*) scrub, (*b*) rain-forest.

4.—Fluviatile and limnological: rivers, ponds, swamps (exclusive of mangroves) and Lake Tungano on Rennell.

5.—Cultivations : (*a*) coconut estates ; (*b*) native gardens.

6.—Rocks, boulders, cliffs and cuttings.

1.—*Littoral.*

(*a*). There are two atolls, Ontong Java or Luangiua 115 miles north of Isabel, and Sikaiana or Stewart Island 125 miles east of the north end of Malaita. Both are inhabited by Polynesians in contradistinction to the bulk of the other islands, which support only Melanesians.

The artificial islands along the western coast of Malaita, whose axis is north-west to south-east, are composed of transported blocks of coral on which coconut palms have been planted.

(*b*) Swamps of mangrove (*Rhizophora*) form a barrier along the coast of many islands and their stilted roots impede progress. Clear passages occur in them, in places wide enough for an out-board motor-boat. Clusters of these trees may be so dense as to be indistinguishable from small islands with soil.

(*c*). The shore or strand flora is characterised by the creeper *Ipomea pes-capreae* and such trees as *Thespesia populnea, Barringtonia speciosa, Casuarina equisetifolia, Scaevola koenigii* and *Tournefortia argentifolia.*

2.—*Guadalcanal grass-plains.*

These have been referred to in some detail above and lie in the dry zone with a rainfall of only 60 to 85 inches. They are burnt annually, and radiation from the bare surface is intense, the temperature ranging from 65° to 104°F.

3.—*Mountains.*

Only one island, Guadalcanal, reaches the height of 8,000 ft., and it is also alone in having a large area over 3,000 ft. Kolombangara is the next highest, with a summit just over 5,000 ft. ; Malaita and San Cristobal reach 4,000, and Isabel just fails to do the same. No meteorological records have been kept in the interior in any of the islands, whose fauna has even yet scarcely been touched. The jungle plants are essentially of the New Guinea type and no endemic genus is known.

4.—*Fluviatile.*

As the islands are on the average less than 15 miles wide (San Cristobal and Guadalcanal reach a breadth of 25 miles), all the rivers are short, as the high watersheds divert them. The tropicopolitan *Coix lachryma-jobi* is found along most rivers, which vary in size and volume in a few hours according to the amount of rain in the mountains. The only malarial mosquito (*Anopheles punctulatus*, Dönitz) in Melanesia breeds normally in temporary collections of water, but has been found also in a semi-permanent swamp in the Three Sisters, north of San Cristobal.

5.—*Cultivations.*

(*a*) Coconuts are the only crop grown by Europeans, as although rubber is planted it does not pay to tap, and tariff-walls check the export of bananas. The estates (whose distribution is marked on the accompanying map) support an entirely alien flora, such as *Sida acuta, S. rhombifolia, Mimosa pudica, Triumfetta bartrami, Chrysopogon aciculatum, Asclepias curassavica, Stachytarpheta jamaicensis* and, in the western part of the Protectorate, *Clidemia hirta*, which is controlled to some extent in Fiji by the West Indian thrips *Liothrips urichi*, Karny.

(*b*). Native crops include taro (*Colocasia*), yams, sweet potato and sugar, and the introduced cassava and tobacco are grown to some extent. Groves of ivory nut (*Metroxylon salomonense*) and betel palms (*Areca catechu*) are planted, but the former palm takes some 15 years before the fruit ripens, after which the tree dies. Agriculture among the Melanesians is not at a very high level, though terraces for irrigating taro were formerly constructed on Guadalcanal, New Georgia and Kolombangara[4]. More trouble is taken by the Polynesians, whose womenfolk plant the taro in irrigated ground previously bedded up with rotting leaf-mould. These people also prepare both a drink (toddy) and toffee from the tapped inflorescence of the coconut.

6.—Rocks and boulders in the higher reaches of the rivers are selected by the pygmy locusts, *Hyboella leveri*, Günth., and *Paratettix macrophthalmus*, Günth.

Brontispa froggatti, Sharp, and its Biological Control.

The Hispid beetle *Brontispa froggatti*, Sharp, is a pest of the unfolded leaves of young coconut palms, the introduced Malayan ones suffering more than local palms whose pinnae are less loose[5]. As large areas have been planted of the less resistant Malayan palms it was decided to introduce the Eulophid, *Tetrastichodes brontispae*, Ferr., from Java, as forecast in 1934[6]. This parasite had already been sent from Java, where it parasitises *B. longissima*, Gestro, to Celebes in order to control the insular form *B. froggatti selebensis*, Gestro. An attempt was made to send parasitised pupae from Java to Sydney, and Celebes to Brisbane, but the cold and long journey proved fatal. Accordingly, another consignment was sent to Rabaul, New Britain (Mandated Territory of New Guinea), where it was kept in cold storage by the Government Entomologist until the writer could proceed there to return with it to the Solomon Islands. Owing, however, to infrequent communication, the time between its arrival in New Britain from Java and its reception in Rabaul by the author, entailed too long a period in cool storage to admit of the emergence of the parasites. The only remaining method was to have the material sent by air mail from the East Indies to Brisbane, and this journey of 4,000 miles, plus a sea-voyage of an additional 1,500 miles, resulted in the parasites arriving in a viable condition. The liberation was made in August and September 1936 on Banika Island in the Russell Group, some 40,000 parasites being released in a block of ten-year-old palms.

The development of *Tetrastichodes* within the pupa takes 16 to 23 days (letter from Director of Klapperproefstation, Celebes) with an average of 18 days. An average of 18 to 20 parasites, with a maximum of 35, may emerge from one *Brontispa* larva or pupa[7].

Lyperosia exigua, de Meij., and its Biological Control.

The buffalo-fly, *Lyperosia exigua*, de Meij., is believed to have reached the British Solomon Islands via New Britain prior to 1923[8] and has now a fairly wide local distribution. In 1933 an attempt was made to exercise some control by liberating a small colony of the Pteromalid, *Spalangia cameroni*, Perk., sent from Fiji[6]. As this parasite is known to have a catholic range of hosts, it was decided to introduce the Javanese *S. sundaica*, Graham, which is more restricted in its hosts, and had been introduced from the East Indies to the Northern Territory of Australia in 1933.

A consignment of 2,500 parasitised pupae was prepared by the Entomological Division of the Council for Scientific and Industrial Research near Darwin and sent by air 2,000 miles to Brisbane and thence 1,500 miles in the cool chamber of the six-weekly mail boat to the Solomon Islands. The liberation was made in June 1936 on Guadalcanal near the stock-yards of a coconut plantation. The chief difficulty was the ant *Pheidole oceanica*, Mayr, which frequents every cake of cow-dung, in which *Lyperosia* breeds. It was found necessary to construct small tables whose supporting columns were smeared with tanglefoot, the dung being placed on the tables and the ants already in possession killed with a sprayer before the delicate *Spalangia* were released. It was noticed that the worker ants seized and killed the parasites if this precaution was not taken. The ant in question has been in the Solomons at least since 1916[9] and is in practically all the islands a thorough scavenger.

Amblypelta cocophaga, China, and immature Nutfall of Coconuts.

This Coreid bug causes the death of young coconuts both prior to and after protrusion of the stigma. It has been possible to induce nutfall both in the laboratory and in the field by enclosing a number of nymphal and adult *Amblypelta* in a cage. Under laboratory conditions an inflorescence was placed in a nutrient solution and the immature nuts had either fallen off or were loose in two to three days where the insects were present but perfectly firm in the case of controls. Further, sections of the nuts under the former conditions showed a brown discoloration in contradistinction to the normal white appearance of the controls. In the field, cages of wire gauze, large enough to envelop the whole of a recently-burst spadix, were employed and a nutfall of 90 per cent. was obtained with the insects inside as against only 70 per cent. in the control cages without *Amblypelta*[10].

It is hoped to introduce the Pteromalid, *Ooencyrtus malayensis*, Ferr., which is a parasite of *Leptocorisa* on rice in the Malay States[11] and of *Dasynus* (a very close ally of *Amblypelta*) in Bangka (east of Sumatra), where it does similar injury to the fruit of pepper that *Amblypelta* does to coconut[12]. A further host of *Ooencyrtus* in Java is *Homoeocerus* on Leguminosae (letter from the Director, Instituut voor Plantenziekten, Java).

A Eupelmid, *Anastatus axiagasti*, Ferr., has been taken on Kolombangara Island on a jungle tree (*Macaranga tanarius*), but there is no danger of co-parasitism if *Ooencyrtus* were to be liberated in the coconut plantations, which are relatively clear of undergrowth.

Insect Pests of Economic Plants.

Bananas are attacked by *Nacoleia octasema*, Meyr., which is parasitised by a species of *Apanteles*. The fruit is also punctured by the proboscis of the Noctuid *Lagoptera regia*, Drury.

The betel palm (*Areca catechu*) is attacked by *Tirathaba rufivena*, Wlk., *Brontispa froggatti*, Sharp, and a weevil, *Meredolus cocotis*, Mshl. On cotton, three species of *Dysdercus* are recorded, viz., *D. decussatus*, Boisd., *D. cingulatus*, F., and *D. sidae*, Montr., the last of which also occurs on kapok, which is further subject to *Lygaeus familiaris*, F. The only pest on rice is the non-swarming grasshopper, *Oxya gavisa*, L., which eats the leaves. The almost universal *Cylas formicarius*, F., is a pest of sweet potato, and a Capsid, *Engytatus tenuis*, Reut., is found on the isolated atoll of Sikaiana where it frequents the sticky lower surface of the leaves of tobacco. Attempts to grow tung trees did not succeed, as *Aleurites fordii* failed to withstand the equatorial climate, which seems more adapted to *A. montana*. The former has its leaves eaten by the Cassidine beetles, *Aspidomorpha guérini*, Boisd., and *A. australasiae*, Boisd., var. *douai*, Boh. One of the main native crops, *Colocasia esculentum* (taro), has its tubers prone to attack from the Dynastid beetles, *Papuana armicollis*, Frm., *P. inermis*, Prell, and *P. hübneri*, Frm. The leaves are eaten by the larvae of the widely-ranging Sphingid *Hippotion celerio*, L.

The Melastomaceous plant, *Clidemia hirta*, is so far confined to Shortland Island, south of Bougainville. As this area has a rainfall of about 145 ins. it is not a likely one for effective control by the thrips, *Liothrips urichi*, Karny, whose numbers in Fiji are considerably checked by heavy rainfall, which also leads to renewed growth of the weed[13]. Experiments have accordingly been begun with a flame-thrower of the type used in Australia for control of lantana and bracken. A small green weevil (*Trigonops* sp.) causes a shot-hole appearance to the leaves but does not appear to exercise any true control.

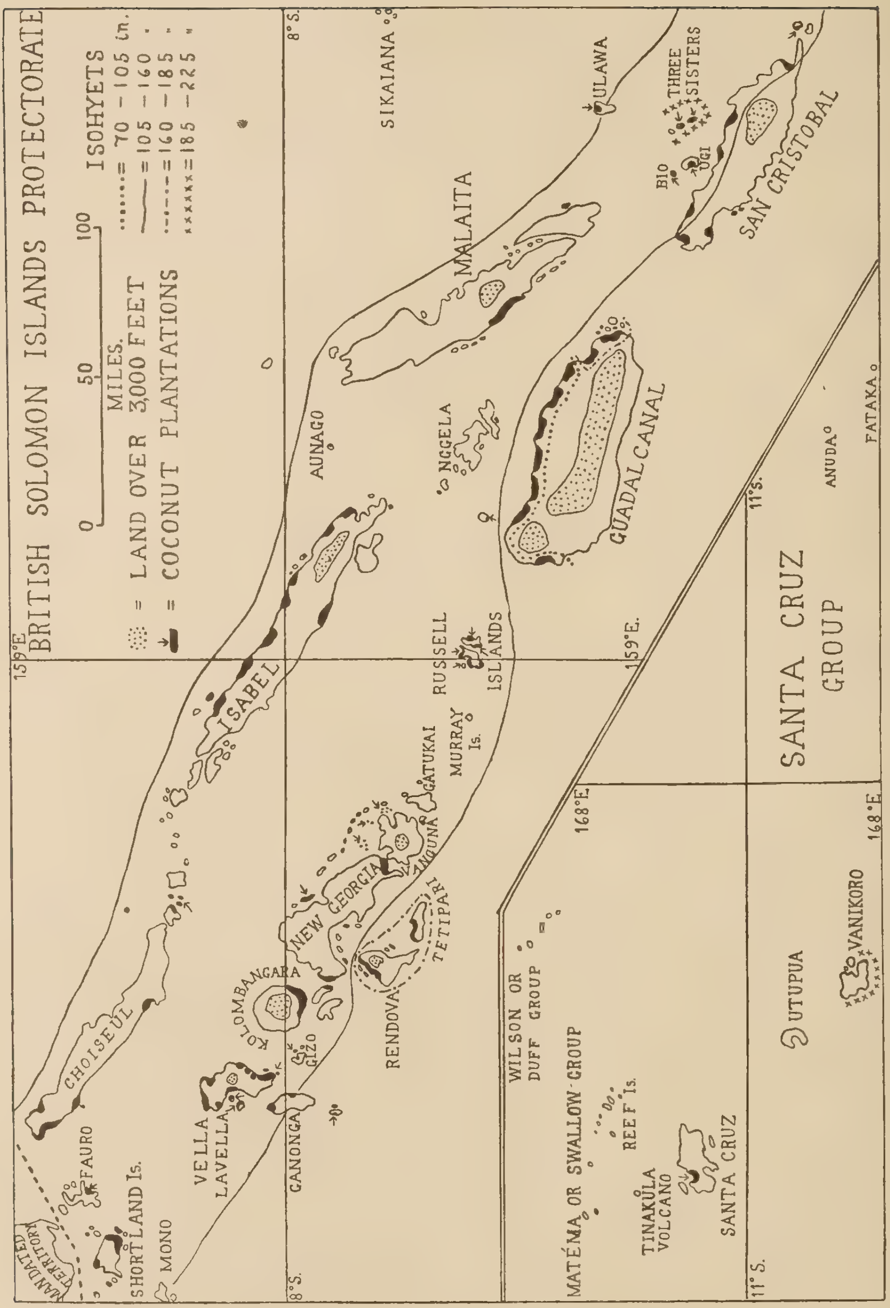
BRITISH SOLOMON ISLANDS PROTECTORATE
0 50 100
MILES.
= LAND OVER 3,000 FEET
= COCONUT PLANTATIONS
ISOHYETS
.......= 70 – 105 in.
——— = 105 – 160 "
-.-.-.= 160 – 185 "
xxxxx = 185 – 225 "
159°E.
8°S.
11°S.
168°E.
MANDATED TERRITORY
FAURO
SHORTLAND Is.
MONO
CHOISEUL
VELLA LAVELLA
GANONGA
KOLOMBANGARA
GIZO
NEW GEORGIA
RENDOVA
TETIPARI
VANGUNA
GATUKAI
MURRAY Is.
RUSSELL ISLANDS
ISABEL
AUNAGO
NGGELA
GUADALCANAL
MALAITA
SIKAIANA
ULAWA
BIO
UGI
THREE SISTERS
SAN CRISTOBAL
ANUDA
FATAKA
SANTA CRUZ GROUP
WILSON OR DUFF GROUP
MATÉMA OR SWALLOW GROUP
REEF Is.
TINAKULA VOLCANO
SANTA CRUZ
UTUPUA
VANIKORO

Fig. 3.

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A NOTE ON THE UTILISATION OF POLYSACCHARIDES BY A GRASSHOPPER.

By A. W. A. Brown.

The following experiments were made in an attempt to show roughly to what extent a leaf-eating insect, feeding under conditions as natural as possible, may utilise the more common polysaccharides. To this end a certain proportion of the particular polysaccharide was added to the normal food, followed by a determination of the amount passed into the excreta.

Material and Methods.

The grasshopper used was *Melanoplus bivittatus*, Say, the eggs being collected at Brandon, Manitoba, and reared in the laboratory on California lettuce ; there was high mortality in the earlier instars only.

The nutrition experiments were conducted in cages made of copper mesh on a wooden framework, with sliding glass front and sloping three-ply floor, of capacities up to 1·6 cu. ft. Diets consisted of finely chopped lettuce—9 parts (wet weight), and the particular polysaccharide—1 part (dry weight). Fresh lots were administered daily on large microscope slides. The diets were made up afresh every 3 days, being kept in a refrigerator. Distilled water was given separately, being changed every 3 days. The excreta, which were scattered on the floor of the cage and dried almost immediately, were collected every 6 days and put in a desiccator.

Experiments were run for 1–2 weeks, each (similar) cage containing the same number of insects in the same stage of development ; only the added polysaccharide being varied. At the termination the number of insects remaining was counted, and the excreta were freed of foreign matter, dried to constant weight, and weighed preparatory to analysis.

The starches and dextrin were estimated by the direct acid hydrolysis method for starch in feeding stuffs, gum acacia by the official method for pentosans, and agar by the tentative method for galactan—all of the A.O.A.C. (1925). Inulin and pectin were determined gravimetrically by alcohol precipitation, and glycogen by acid hydrolysis of the alcohol precipitate.

Results.

The percentages of the various polysaccharides emerging in the excreta, and their effect on the insects, are summarised in Table I. (For technical reasons, 5 parts of water were added to the dextrin diet, and pectin was administered in 1 part to 18 of lettuce, with 10 parts of water.)

The unassimilability of intact starch grains is remarkable, the excreta being quite white, and resembling a hyaline bag enclosing the intact granules. The amount of agar passed in the excreta appeared, from the amount, size and behaviour in water of the excretory pellets, to be almost as much as in the case of inulin, although the yield of mucic acid was inordinately low. No trace of excreted monosaccharides could be detected by a variety of qualitative tests. There is a considerable amount of excretion of starch and pentosan on a diet of lettuce alone.

TABLE I.

Utilisation of various Carbohydrates by Grasshoppers.

Substance in diet	% of substance in excreta	Condition of insects
Starch grain (potato) ...	60·9	Normal, voracious.
Starch grain (arrowroot) ...	57·6	Normal, voracious.
Inulin	41·7	Normal, very voracious.
Agar	(1·3)	Normal, very voracious.
Dextrin	39·8	Undersized, eating little.
Pectin	35·8	Undersized, normal appetite.
Soluble Starch	28·1	Oversized, vigorous.
Gum Acacia	12·7	Undersized, scarcely eating.
Glycogen	10·1	Normal.
Glucose	0·0	Normal, eating little.
Galactose	0·0	Normal, eating little.
Xylose	0·0	High mortality, excreta with fluid.
Control Starch	13·6	(On ordinary diet of lettuce alone.)
Control Pentosan	9·5	

Results of individual experiments are summarised in Table II. To obtain comparative weights of excreta, a correction factor: $\dfrac{\text{Initial no. of insects.}}{\frac{1}{2}\,(\text{Initial no.} + \text{Final no.})}$ was applied. The high excretion on the unassimilable but non-harmful diets (starch grains, inulin, agar) is very marked. In the case of the added monosaccharides, the insects require to ingest far less unassimilable material for adequate nourishment (Expt. 6).

TABLE II.

Details of Experiments.

Substance in diet	Wt. excreta mg.	Final no. of insects	Corrected wt. excreta, mg.	% substance in excreta	Wt. substance excreted, mg.
Expt. 1. 120 nymphs, 5th instar, 8 days duration.					
Potato starch	1,233	97	1,364	60·9	831
Arrowroot starch ...	1,271	99	1,392	57·6	802
Control ... (Lettuce only)	779	98	866	13·6	118
Expt. 2. 19 adults and 6th instar nymphs, 10 days duration.					
Inulin ...	1,548	14	1,742	41·6	725
Soluble starch	481	13	571	28·2	161
Dextrin ...	719	17	759	32·1	244
Expt. 3. 14 nymphs, 6th instar, 13 days duration.					
Pectin ...	55	6	77	38·3	30
Agar ...	808	10	942	(1·5)	(14)
Inulin ...	1,347	10	1,571	40·8	641
Gum acacia	61	5	90	12·7	11
Expt. 4. 13 adults and 6th instar nymphs, 11 days duration.					
Agar ...	787	10	890	(1·3)	(12)
Pectin ...	186	10	210	33·2	70
Glycogen ...	566	12	588	10·6	62
Expt. 5. 40 nymphs, 6th instar, 13 days duration.					
Soluble starch	848	32	942	29·4	277
Dextrin ...	224	28	264	39·8	105
Expt. 6. 20 nymphs, 6th instar, 16 days duration.					
Glucose ...	29	5	46	0·0	
Galactose ...	34	6	52	0·0	
Xylose ...	40	1	76	0·0	
Control ... (Lettuce only)	291	9	401	0·0	

Discussion.

From the above results it is apparent that although monosaccharides are readily absorbed by the grasshopper, their polysaccharide polymers are passed through the gut with little or no change. Ullmann (1932) had demonstrated that the intestinal juices of a number of phytophagous insects are unable to digest the starch granule, but can quickly hydrolyse boiled " soluble " starch ; these experiments therefore bring confirmatory evidence from another angle of approach. Soluble starch, however, is only partly utilised ; indeed, the grasshopper appears to be a very wasteful feeder as regards polysaccharides, even a substance so readily assimilable as glycogen being excreted in significant amounts. In view of its relation to bee dysentery (Phillips, 1927) the fact that dextrin was excreted in greater amounts even than was soluble starch, and had a deleterious effect on the insect, seems noteworthy.

Protein, however, was found to be entirely absent from the excreta of *Melanoplus* (Biuret, Millons, etc.). Therefore the above results bear out the thesis of Hering (1926), based mainly on the findings of Haberlandt (1918), namely, that in leaf-eating insects the chief dietary factor is protein, which is completely utilised along with the soluble sugars, while polysaccharides are excreted for the most part unchanged.

These experiments were carried out in the Department of Biochemistry, University of Toronto, and completed at the London School of Hygiene and Tropical Medicine during the tenure of a Royal Society of Canada Fellowship.

Summary.

1. All polysaccharides fed to *Melanoplus* have been utilised incompletely or not at all.

2. Rupture of the starch granule renders it partly utilisable.

3. Glucose, galactose and xylose are completely absorbed.

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COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st January and 31st March, 1937.

Mr. A. M. ADAMSON :—36 Diptera, 5 Coleoptera, and 6 Parasitic Hymenoptera ; from the British West Indies.

AGRICULTURAL RESEARCH SERVICE, KHARTOUM :—50 Coleoptera, 400 Parasitic Hymenoptera and 2 species of Coccidae ; from the Sudan.

AUSTRALIAN MUSEUM, SYDNEY :—28 Curculionidae ; from Melanesia.

Mr. P. N. KRISHNA AYYAR :—37 Coleoptera and 93 Parasitic Hymenoptera ; from South India.

Dr. H. F. BARNES, Rothamsted Experiment Station :—3 Parasitic Hymenoptera ; from England.

BERNICE P. BISHOP MUSEUM :—4 Curculionidae ; from the Pacific Islands.

Dr. H. BLUNCK :—5 Parasitic Hymenoptera ; from Germany.

Dr. G. BONDAR :—6 Diptera and 11 early stages, 152 Coleoptera and 3 early stages, and 16 Lepidoptera ; from Brazil.

Mr. P. BOVEY :—50 Curculionidae and 150 Parasitic Hymenoptera ; from Switzerland.

Mr. B. D. BURKS :—7 Parasitic Hymenoptera ; from the United States of America.

Mr. E. BURTT :—568 Orthoptera ; from Tanganyika Territory.

Prof. P. A. BUXTON, London School of Tropical Medicine :—7 Tabanidae ; from Trinidad.

CANE HILL HOSPITAL, COULSDON :—20 Formicidae ; from England.

Mr. F. G. CHEN :—4 Coleoptera, 16 Lepidoptera, and 12 Rhynchota ; from China.

CHIEF ENTOMOLOGIST, PRETORIA :—3 *Haematopota*, 10 other Diptera, 57 Coleoptera, 53 Parasitic Hymenoptera, and 5 Aegeriidae ; from S. Africa.

Mr. A. F. CLARK :—2 Coleoptera ; from New Zealand.

Mr. G. H. CORBETT, Government Entomologist :—19 Diptera, 51 Coleoptera, 27 Parasitic Hymenoptera, 9 Formicidae, 44 Lepidoptera, 37 Rhynchota, 2 Orthoptera, and 14 Dermaptera ; from Malaya.

CORYNDON MEMORIAL MUSEUM, NAIROBI :—60 Blattidae and 130 Dermaptera ; from East Africa.

Mr. A. CUTHBERTSON, Entomologist :—16 Coleoptera and 1,500 Isoptera ; from Southern Rhodesia.

Mr. R. C. M. DARLING, Locust Investigator :—142 Orthoptera ; from the Sudan.

Mr. M. DELASSUS :—6 Parasitic Hymenoptera ; from Algeria.

Mrs. H. R. P. DICKSON :—8 Coleoptera and 2 Orthoptera ; from Arabia.

DRESDEN MUSEUM :—8 Coleoptera ; from New Zealand.

Mr. D. VESEY FITZGERALD, Entomologist :—22 Coleoptera and 10 early stages, 3 Parasitic Hymenoptera, 8 Lepidoptera, and 2 Chrysopidae ; from the Seychelles.

Dr. L. FULMEK :—6 Parasitic Hymenoptera ; from Austria.

Mr. J. C. M. GARDNER, Systematic Entomologist :—65 Coleoptera and 24 Lepidoptera ; from the United Provinces, India.

Prof. B. A. R. Gater :—32 Isoptera ; from the Straits Settlements.

Government Entomologist, Coimbatore :—25 Coleoptera, 10 Lepidoptera and 6 slide preparations, and 4 Rhynchota ; from South India.

Government Entomologist, Lyallpur :—5 Diptera, 25 Coleoptera, 104 Parasitic Hymenoptera, 18 Lepidoptera, 1 species of Coccidae, 100 Mites, and a tube of Nematoda ; from the Punjab, India.

Government Entomologist, Mandalay :—8 Coleoptera ; from Burma.

Mr. G. L. R. Hancock :—6 Curculionidae ; from Uganda.

Mr. E. Hargreaves, Government Entomologist :—200 Coleoptera and 50 early stages, 34 Parasitic Hymenoptera, 500 Formicidae, 80 Thysanoptera, and 20 Mites ; from Sierra Leone.

Mr. W. V. Harris, Entomologist :—11 Lepidoptera ; from Tanganyika Territory.

Mr. G. F. Hill :—80 Isoptera ; from the Solomon Islands.

Imperial Entomologist, New Delhi :—16 Coleoptera, 13 tubes of Aleurodidae, and 100 Mites ; from India.

Indian Museum, Calcutta :—801 Coleoptera ; from India.

Institute for Plant Diseases, Buitenzorg :—7,512 Parasitic Hymenoptera ; from the Dutch East Indies.

Mr. C. B. R. King :—150 Mites ; from Ceylon.

Mr. T. W. Kirkpatrick, Entomologist :—19 Parasitic Hymenoptera ; from Tanganyika Territory.

Mr. C. D. Knight :—181 Coleoptera and 150 Rhynchota ; from Kenya Colony.

Miss J. Laing :—27 Parasitic Hymenoptera and 28 cocoons ; from England.

Leicester Museum :—8 Coleoptera ; from England.

Mr. R. A. Lever, Government Entomologist :—7 Culicidae, 4 Tabanidae, 53 other Diptera, 135 Coleoptera, 20 Parasitic Hymenoptera and 3 cocoons, 69 other Hymenoptera, 1 species of Aphidae, 120 other Rhynchota, 10 Mallophaga, 4 Scorpions, 3 Intestinal worms, and 10 Earthworms ; from the Solomon Islands.

Mr. C. J. Louwerens :—146 Coleoptera ; from Java.

Prof. F. J. Meggitt :—247 Coleoptera, 10 Psychidae and 20 early stages, 17 Rhynchota, and 35 Orthoptera ; from Burma.

Mr. C. Menozzi :—21 Parasitic Hymenoptera ; from Italy.

Dr. D. Miller, Cawthron Institute :—6 Rhynchota ; from New Zealand.

Mr. H. M. Morris, Government Entomologist :—330 Coleoptera, 31 Parasitic Hymenoptera, 330 Rhynchota, and 15 Orthoptera ; from Cyprus.

Mr. J. Muggeridge, Government Entomologist :—8 Diptera, 14 Parasitic Hymenoptera, and 3 Lepidoptera ; from New Zealand.

Musée du Congo Belge :—16 Curculionidae and 22 Parasitic Hymenoptera ; from the Belgian Congo.

Dr. J. G. Myers :—49 Diptera and 46 early stages, 25 Coleoptera and 4 larvae, 30 Parasitic Hymenoptera, and 6 Rhynchota ; from Haiti.

Mr. N. S. Noble :—31 Parasitic Hymenoptera ; from New South Wales.

Mr. F. B. Notley, Entomologist :—1 Scolytid ; from Tanganyika Territory.

Oxford University Museum :—3 Parasitic Hymenoptera ; from Greenland : and 241 Curculionidae ; from the New Hebrides.

Mr. E. F. Peck, Veterinary and Agricultural Officer :—2 Lepidoptera and 250 Orthoptera ; from British Somaliland.

Mr. R. H. Phillips :—265 Lepidoptera ; from the Fiji Islands.

Pullman Car Co., Ltd. :—20 Lepidopterous early stages ; from England.

Mr. P. Regnier :—114 Parasitic Hymenoptera and 23 Orthoptera ; from Morocco.

Mr. E. Rivnay :—74 Coleoptera ; from Palestine.

Selangor Museum :—159 Coleoptera ; from Malaya.

Nihat Shevket :—88 Diptera and 1 species of Coccidae ; from Asiatic Turkey.

Mr. H. W. Simmonds, Government Entomologist :—4 Parasitic Hymenoptera and 7 Formicidae ; from the Fiji Islands.

Prof. C. Strickland :—1 Sarcophagid, 1 Chalcid, and 100 Curculionidae ; from Calcutta, India.

Mr. J. Suire :—12 Parasitic Hymenoptera ; from France.

Mr. E. L. Taylor :—3 Anoplura and 36 Mites ; from England.

Mr. T. H. C. Taylor, Entomologist :—2 Diptera, 7 Coleoptera, 59 Lepidoptera, and 2 Rhynchota ; from Uganda.

Mr. A. Théry :—11 Curculionidae ; from Algeria.

Mrs. Thompson :—8 Coleoptera and 5 Rhynchota ; from Tanganyika Territory.

Turkish Sugar Factory :—3 Parasitic Hymenoptera ; from Turkey.

Dr. F. van Emden :—340 Coleoptera and 400 early stages ; from various localities.

Mr. F. G. S. Whitfield, Medical Entomologist :—314 Culicidae, 3 Tabanidae, 2 Hippoboscidae, 224 other Diptera, 4 Coleoptera, 3 Parasitic Hymenoptera, 2 other Hymenoptera, 7 Lepidoptera, 2 Cimicidae, 2 other Rhynchota, 6 Orthoptera, and 4 Dermaptera ; from the Sudan.

Mr. F. X. Williams :—1,100 Diptera and 9 larvae, 5 Coleoptera, and 118 Rhynchota ; from Hawaii.

Zoological Museum, Vienna :—1,272 Braconidae ; from Austria.

THE INSECT PARASITES OF THE SPRUCE SAWFLY (*DIPRION POLYTOMUM*, HTG.) IN EUROPE.

By

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Introduction.

In 1930 a severe outbreak of the Spruce Sawfly, *Diprion* (*Lophyrus*) *polytomum*, Htg. (*hercyniae*, Htg.), was discovered over a large area in the centre of the Gaspé Peninsula in eastern Quebec, Canada. The insect was doing very severe damage to valuable stands of Black and White Spruce (*Picea mariana* and *P. canadensis*) through defoliation of the trees by its larvae. In the following year it had increased considerably and it was estimated that 2,000 square miles of forest were badly damaged. By 1933 the area of severe damage had increased to 4,000 square miles. The sawfly continued to spread at this alarming rate until in 1936 the area of severe damage covered approximately 10,000 square miles and the range of the insect had extended southward through the United States into Connecticut (specimens have been captured not far from New York), westward as far as Lake Temiskaming in Ontario, and northward across the St. Lawrence River to Lake St. John. It now constitutes one of the most serious and dangerous forest pests ever introduced into North America.

D. polytomum is a native of Europe, where it has an extremely wide distribution, being found over the whole range of Spruce (*Picea excelsa*) from Finland to Jugoslavia, but where it never causes any serious damage to the forests, being, on the whole, a comparatively rare insect, except under certain favourable sets of conditions. Under the most favourable conditions, however, it never attains anything approaching the abundance of any of the common European forest pests. The reason for this tremendous and rapid increase in Canada is probably twofold. Firstly, the sawfly is reproducing parthenogenetically in Canada, males being almost unknown, whereas in Europe it is normally bisexual with the sexes in general in approximately equal proportions. The effect of this is virtually to double the reproductive rate in Canada. Secondly, as is usually the case with accidentally imported insects, the sawfly arrived in Canada without any of its natural enemies and up to the present no native parasites have been found attacking it in its new environment. This state of affairs led to a request, in 1932, from the Canadian Government to Farnham House Laboratory, for a study to be made of *D. polytomum* in Europe with the object of collecting and sending such of its natural enemies, especially insects, as might be considered of possible value in helping to check the spread and ultimately reduce the infestations in Canada.

The work commenced at once, and by the autumn of 1932 a large part of Saxony and Bohemia had been searched for the sawfly, five different collecting points had been located and between five and six thousand larvae and cocoons collected. A number of these were used for studying the insect parasites, but 3,267 cocoons were sent to Canada that winter. The results of this and subsequent years' investigations showed that many of the major parasites of *D. polytomum* occur also on other species of the genus *Diprion*, which frequently appear in great numbers in Europe. Laboratory tests at Farnham House and field tests in Canada showed that the parasites from other hosts will usually attack the Spruce Sawfly, so from this time on, although the main efforts were always concentrated on the collection of *D. polytomum*, outbreaks of other species showing suitable parasitism were always sought. In this way it was possible to make very large collections of some parasites, which could never have been obtained in any quantities from the never numerous Spruce Sawfly. In 1932, 5,202 cocoons of *D. polytomum* and 1,550 heavily parasitised cocoons from a mixed infestation of *D. sertifer*, *D. frutetorum*, and *D. virens* were sent to Canada. In the succeeding years there was a tremendous increase in the collections of both *D. polytomum* and other species, partly through increased efficiency because of experience gained and getting to know the people and countries in Central Europe, but mainly through the increased funds made available by the Canadian Government. With this extra money it was possible to get together and train a team of men for collecting *D. polytomum* in Czechoslovakia, where, for several reasons, all the collections of this species have been made. In 1934 only four such men were employed, but by 1936 nearly 30 men had been trained and over 20 were working in the field at once. This enabled the Entomologists from Farnham House, who had previously been fully occupied with collecting, to devote more time to the scientific side of the work and to locating and collecting material of other hosts from other countries. Actually in 1936, the chief of the team of collectors, a very able Russian, Dr. L. Černosvitov, was left in charge of the collecting of *D. polytomum* for most of the summer and only one Entomologist went out from England, whereas hitherto it had always been necessary to employ two on this work. The search for outbreaks of other species of *Diprion* has led from Sweden to the Adriatic coast, and the main collections, in all cases of *D. sertifer*, have been made in Hungary, Czechoslovakia and Sweden. The numbers of cocoons collected and despatched from Europe during the last three years is given below. Most of this material has been sent on to Canada from Farnham House, only small samples having been retained for study.

Year	*D. polytomum* cocoons	*Diprion* spp. (mainly *sertifer*)	Eggs of *D. sertifer*
1934	15,364	4,405,179	—
1935	55,716	1,713,750	391,160
1936	202,267	20,858,241	161,950

With the 1932 and 1933 shipments this makes a total of 281,916 *D. polytomum* and 27,531,830 *D. sertifer*, etc., together amounting to 27,813,746 cocoons and eggs, containing from 25 per cent. to 80 per cent. parasites.

This work is still being continued, but it is considered advisable at this point to summarise and put on record some of the immense amount of data and information gleaned on such an undertaking. The present paper has a purely practical aim, of recording all the insect parasites found attacking *D. polytomum* in that part of Europe where our work lay, to give brief but sufficient descriptions to facilitate the recognition of the adult forms by the practical worker, and in the case of all the primary parasites to give, so far as we are able, some account of their biology and descriptions of the larval stages sufficient for recognition. Finally, notes are added for each species, giving our own opinion as to its suitability or not for introduction into Canada and its prospects of success.

The constant travelling in many countries of Europe which this work has involved has brought us into contact with a great number of people, both scientists and others, and has left us with many very good friends. To all these friends we are indebted for their invariable courtesy and help, which has done so much to make our work both pleasant and successful. We should like to express our gratitude more especially to Professor Julian Komárek and his staff, particularly Dr. Anton Pfeffer, of the Forest Protection Institute in Prague, where for five years we have had our headquarters; to Professor Ivar Trägårdh and his staff of the Skogsförsöksanstalt in Sweden, for his help in making big collections of *D. sertifer* cocoons and eggs in 1935 and 1936; to Professor Bako and his staff of the Növényvédelmi Kutátó Intézet in Budapest, our biggest collections of *D. sertifer* having come from Hungary in 1934, 1935, and 1936; and to Professor Heinrich Prell of Tharandt Forstliche Hochschule, where our first investigations on *D. polytomum* were successfully started.

2. Previous Records of Parasites.

Previous to the present work only 12 species of parasites had been recorded from *D. polytomum*. These records gave no exact data as to the life-histories or interrelationships of the parasites, and frequently it was not even stated whether they were primary or secondary upon this host. Only the commonest species had been studied in any detail, and then only in their occurrence on other hosts, such as *Exenterus marginatorius* on *Diprion pini* and *D. sertifer*, and *Sturmia inconspicua* on certain Lepidoptera. In the light of our present investigations we cannot accept even this information as invariably correct ; for example, Sitowski (1925) states that *Exenterus marginatorius* lays its eggs *in* the body of *D. sertifer* and that development is internal. The following is the list of the previously recorded parasites of *D. polytomum* :—

HYMENOPTERA :

ICHNEUMONIDAE :

Cryptinae :	*Habrocryptus* (*Caenocryptus*) *polytomi*, Tschek (De Gaulle, 1908).
Ophioninae :	*Holocremnus ratzeburgi*, Tschek (Schmiedeknecht, 1908 ; Forsius, 1932).
Tryphoninae :	*Exenterus tricolor*, Roman (Forsius, 1932).
	Exenterus marginatorius, F. (Forsius, 1932).
	Lamachus spectabilis, Holmgr. (Forsius, 1932).
	Mesoleius vepretorum, Grav. (Giraud, 1877).
	Mesoleius multicolor, Grav. (De Gaulle, 1908).
	Mesoleius multicolor var. *dives*, Holmgr. (Giraud, 1877).
	Tryphon laevis, Ratz. (André, 1879–81).

DIPTERA :

TACHINIDAE :	*Diplostichus janithrix*, Htg. (Baer, 1920).
	Ptychomyia selecta, Mg. (Baer, 1920).
	Sturmia inconspicua, Mg. (*bimaculata*, Htg.) (Baer, 1920).

3. Parasites met with in the Course of the present Work.

The following 31 species of parasites have been bred from larvae or cocoons of *D. polytomum* during the present work, the majority of the host material having been collected in Czechoslovakia, a small quantity only coming from Saxony, Bavaria, and Austria. It will be observed that half of the parasites previously recorded do not appear here. We are inclined to explain this, in the case of the three species of *Mesoleius* and *Tryphon laevis*, by pointing out that these are very old records and the validity of the identifications can by no means be relied on ; indeed, all our work with the systematics has shown the inadvisability of relying on identifications in previous parasite records. In the case of *Diplostichus janithrix* and *Ptychomyia selecta*, which are recent and certainly reliable records, it is quite likely that our present area of activities has not come within the distribution of these Tachinids.

HYMENOPTERA :

ICHNEUMONIDAE :

		Stage of host attacked.
Cryptinae :	*Microcryptus basizonius* var. *curtulus*, Kr.	Prepupa in cocoon.
	Leptocryptus aereus, Grav.	Hyperparasite.
	Spilocryptus abbreviator, F.	Prepupa in cocoon.
	Spilocryptus abbreviator, var. *hopei*, Grav.	Prepupa in cocoon.

Cryptinae:—*continued.*		
	Habrocryptus polytomi, Tsch.	Prepupa in cocoon.
	Hemiteles areator, Panz.	Prepupa or hyperparasite.
	Hemiteles sordipes, Grav.	Hyperparasite.
	Gelis (*Pezomachus*) *acarorum*, L.	Hyperparasite.
	Gelis sp.	Hyperparasite.
Pimplinae:	*Delomerista* sp.	Prepupa or pupa in cocoon.
	Pimpla alternans, Grav.	Prepupa or pupa in cocoon.
Ophioninae:	*Mesochorus thoracicus*, Grav.	Hyperparasite on larval parasites.
	Mesochorus fulgurans, Curt.	Hyperparasite on larval parasites.
	Mesochorus (?) *dimidiatus*, Hlmgr.	Hyperparasite on larval parasites.
	Holocremnus ratzeburgi, Tschek	Larva.
Tryphoninae:	*Lamachus* sp.	Larva.
	Lamachus spectabilis, Hlmgr.	Larva.
	Exenterus tricolor, Roman	Larva or prepupa before spinning.
	Exenterus adspersus, Hart.	Larva or prepupa before spinning.
	Exenterus marginatorius, F.	Larva or prepupa before spinning.
	Exenterus sp. (near *adspersus*)	Larva or prepupa before spinning.
BRACONIDAE:		
Braconinae:	*Microbracon* sp.	?
CHALCIDIDAE:		
Toryminae:	*Monodontomerus dentipes*, Dalm.	Prepupa in cocoon, rarely hyperparasite.
Pteromalinae:	*Habrocytus* sp.	Hyperparasite.
	Eutelus subfumatus, Ratz.	Prepupa in cocoon.
	Dibrachys cavus, Walk.	Prepupa or hyperparasite.
	Diglochys lophyrorum, Ruschka	Prepupa or hyperparasite.
	(?) *Stenomalus* sp.	?
Eulophinae:	*Pleurotropis* sp.	Hyperparasite.
	Microplectron fuscipennis, Zett.	Prepupa in cocoon, rarely hyperparasite.
DIPTERA:		
TACHINIDAE	*Sturmia inconspicua*, Mg.	Larva.

It is interesting that of the 20 parasites that can act in a primary capacity, at least 5, or one quarter of the number, can also be hyperparasitic. It is especially interesting to see species such as *H. areator* and *D. cavus* acting as primaries.

Thus only 15 species are obligatory primaries and 9 obligatory secondaries. This is undoubtedly due to the host being a Hymenopteron, and certain of the more polyphagous species are ready to victimise the sawfly or its parasites with equal facility. In some cases, however, notably *Microplectron* and *Monodontomerus*, hyperparasitism is the result rather of accident than deliberation, oviposition by these species taking place in a cocoon already containing an immature grub or egg of a primary Ichneumonid parasite. The more quickly developing Chalcids overtake the larger Ichneumonid and finally consume it as well as the true host.

In two cases (*Microbracon* and *Stenomalus*) only a single, rather doubtful individual was obtained and the status is unknown. Nearly two-thirds of the parasites (19 species) attack the host in the cocoon, only 11 species attacking the larvae. Twelve of the primary or facultative primary parasites attack the cocoons and 8 attack larvae. As might be expected, most of the secondaries oviposit in the cocoons, but the three species of *Mesochorus* oviposit in already parasitized larvae. The parasites are dealt with separately in the following section, and their inter-relations with the host and with one another are being dealt with more fully in a later paper.

4. Practical Notes.

Before proceeding with the descriptions of the individual parasites, it is necessary to give some general notes which must be borne in mind when reading the descriptions, also some practical advice as to the preparation of the larvae for examination. This latter is given not only as information, but also in order that the method of preparation of the specimens on which the descriptions and drawings are based may be known. This is important, since preparations can assume very different appearances according to the methods employed.

In no case has a full description of the adult insects been attempted, merely sufficient being given to enable the recognition of the various species among the *D. polytomum* parasites or in their own genera. This is intended mainly for the practical worker in the field, who has not access to a full library. The adult descriptions (and the key) refer always to the females unless explicitly stated. Usually the male is very similar in general coloration and characters, differing only in size and the shape of the abdomen. Wide differences in the sexes are mentioned. The length of the adult is taken from specimens bred from *D. polytomum* and does not include antennae or ovipositor. The size is apt to vary considerably, in the case of the Ichneumonids depending on the size of the host, in which the males are much smaller than the females ; and in the case of the Chalcids depending also on the number of individuals reared from each host.

In dealing with the larvae size is found of little value for recognition for the same reasons, consequently the dimensions of the full-grown larvae are rarely given. The chitinized mouth-parts and tentorium of the larval head afford the best and most easily recognisable characters, these being quite easily seen in the living larva with a hand lens or binocular microscope. The separation of allied tribes and genera, however, usually entails rather finer points of distinction in the mouth-parts and skin structure, and spiracles also. For this, examination of a preparation under the compound microscope is necessary. All the drawings and descriptions have been made from such preparations. It is inevitable that the larval head will be more or less flattened in mounting, and therefore the general appearance of the mouth-parts and tentorium will be somewhat altered, having a rather broader lay-out than in the living larva. The angle at which the head lies on the slide also makes a considerable difference to the appearance. The size, shape, pigmentation and proportions of the different structures, however, remain unaltered. The method of preparation for all our specimens has been identical and therefore the figures are comparable. The method is given below. For description and illustration the spiracles are always taken from the thoracic region of the larvae, although there is not much variation over different parts of the body in the Ichneumonids. The illustrations represent, as near as we can get, the appearance under high magnification, without being diagrammatic or in true optical section. Skin structure is always taken from the mid-ventral area of the first thoracic segment so as to be strictly comparable. Occasionally the skin structure varies over the different segments, and usually in this region it is most developed. Also, some parts of the skin of this region is usually present when the head of the larva is mounted alone.

Since this paper is written mainly from a practical point of view, the life-history and description of the larval stages is given only for the primary parasites of *D. polytomum*. The hyperparasites can all be grouped together as of no value for the project in its present stage. They are easily distinguished from the primary parasites on a careful inspection of the cocoon in which they developed. The larvae of all the primary Ichneumonid parasites, with the exception of *Delomerista* and *Pimpla*, on reaching maturity spin a thin, flimsy cocoon of one or more layers of white or grey papery material, within the host cocoon, the remains of the sawfly prepupa being excluded. If then any larvae are found feeding on anything *inside* this white papery cocoon it is certain they are secondary, this being especially obvious in the case of Chalcids. If the secondaries have reached maturity they spin a second papery cocoon (except the Chalcids), usually excluding that of the primary on which they have fed. Besides this, the remains of the primary larvae can always be found, though sometimes not very easily. If the primary had not reached maturity when it was killed, of course no cocoon will be present, but in this case its remains, together with those of the sawfly prepupa, can always be found on careful search.

In quoting percentages of parasitism for different species on *D. polytomum*, figures are given only when samples of over a hundred specimens, usually considerably more, have been examined. Figures for larval parasites are obtained either from the dissection of the host prepupae or from emergences from cocoons that were spun in captivity, so that there was no loss from competition with the intrinsically superior cocoon parasites or hyperparasites. Figures for cocoon parasites are from emergences from cocoons collected in the field. This is inevitably a less reliable figure than that for larval parasites, always underestimating the true rôle played by the cocoon parasites. As will be pointed out, these usually have more generations in the year than the host, especially the Chalcids, adults being usually present in the field throughout the summer months, owing to overlapping of generations and delayed emergences, so that oviposition on the host cocoons is continually going on. Thus the parasitism will depend entirely on when the samples are collected. Even if the collection is made as late as possible, just before the emergence of the adults, so as to get maximum exposure to parasitism, this will not include some individuals, especially Chalcids with a very quick development, which have already emerged. Thus the figures quoted in the case of the cocoon parasites are the very minimum and by no means represent the full losses inflicted on the host by these factors.

In taking autumn or winter samples of cocoons it is often found tedious or inconvenient to wait until the following spring for emergences. If the cocoons are collected in autumn and placed straight into a warm atmosphere this will in no way accelerate development, emergence taking place, as in naturally situated cocoons, in the following spring, or at most a few weeks earlier. If, however, the cocoons are collected late in winter and then brought into a warmed room, emergence usually takes place considerably earlier. Working on the assumption that exposure to a low temperature for a certain period is necessary for the development of the overwintering parasite eggs or larvae, we have evolved the following simple method of forcing emergence. Cocoons collected or bred in autumn are slowly cooled down to a temperature just above freezing, 1 or 2°C., at which they are held for a month, and then slowly brought to successively higher temperatures until about 26°C. is reached. This so accelerates development that adult parasites and sawflies may be obtained by Christmas, three or four months before the normal time of emergence. The lowering and raising of the temperature must be gradual, lasting over three or four weeks, and the humidity should be kept above 60 per cent. R.H., and care taken not to allow it to increase too much during the cooling process. If the cocoons are treated *en masse*, cardboard or wooden boxes are better containers than metal boxes, as they do not encourage the condensation of moisture. Glass-top boxes are very bad ; gauze-topped boxes are better. For small quantities probably the best containers are short lengths of wide glass tube, plugged at each end with cotton wool. For individual cocoons we always used gelatine capsules. These cannot be subjected to a very high humidity however, for at 70 per cent. R.H. they go soft.

Preparations of parasite larvae can be made either from living larvae themselves, which is vastly easier and preferable, or from the cast skins of mature larvae found in the cocoons from which the parasites have emerged. This latter method was used in every case at the beginning of the work, in order to recognise the larval stages of the different parasites. Preparations from living larvae are best made by keeping the killed larva either in water or in a stoppered glass tube for two to three weeks until the body contents have completely decomposed. Then, on opening the larva, the inside is easily washed away under gently moving water, and the chitinous skin and head structures will be in perfect, undamaged condition. For mounting the whole preparation a mid-dorsal incision should be made the length of the whole body from the tail to the back of the head, then lateral incisions round the base of the head, separating it from the first segment, to which it should remain attached only in the ventral region. In this way the skin can be spread out flat, displaying the spiracles, tracheae and other structures, and the head will assume a position with the chitinous mouth-parts, struts, and arches slightly flattened into a plane more or less parallel with the slide. Alternatively, the head can be cut completely off round the junction with the first segment and mounted separately from the skin. A far quicker method of preparing fresh larvae is to make the dorsal incision and remove most of the body contents first, or cut off the head, and just bring to the boil in a 5 per cent. solution of caustic potash. It should not be boiled for any time or the fine chitinous structures will be lost. If not boiled enough the flesh is difficult to remove. After potash, wash and remove the remaining flesh and muscles with a fine brush or needle. In order to prepare a parasite skin from the cocoon remains, the whole contents of the sawfly cocoon should be placed in a watch glass, the papery cocoon of the parasite removed and the remainder allowed to soak in water for a short while. The last larval skin of the parasite is usually found attached to the little blob of excrement at one end of the parasite cocoon, or mixed up with the cast pupal skin. When removed it is usually found full of bubbles, especially the head-capsule, the most important part. The best way of getting rid of these is by boiling in water. The skin is then soft enough to be carefully stretched out and mounted.

In our experience, by far the best mounting medium is de Faure's solution or Keilin's mixture, into which the preparation can be placed direct from water. If sufficient medium is used the coverslip need not be supported. If desired, it can be supported on tiny pellets of plasticine. This is largely a matter of choice. After the cover-slips are in position, it is important so to manoeuvre the head, by gentle pressure, that the plane in which most of the mouth structures lie is parallel to the slide, otherwise a very distorted and misleading view will be obtained. In these low refractive index media the chitinous structures, even the tiniest hairs and sensillae, show up to the best advantage. We now use exclusively this method of mounting for all preparations of the immature stages, eggs or larvae, finding it gives the best results as well as being the easiest. It can be employed in the field, the slides, cover-slips, bottle of water and of De Faure (all that is necessary) being packed in the microscope box or carried in the pocket. We now never use staining or balsam for mounting, as in it many fine chitinous structures are lost. Eggs and small larvae can be mounted direct in De Faure or Keilin without any previous washing or even killing. In a day or two they are sufficiently clear for the internal structures to be seen. Or the larvae may be brought just to the boil, or merely warmed for a few minutes in 5 per cent. caustic potash solution, washed and mounted, when the internal chitinous structure will be much more clearly brought out. For the examination of Chalcid larvae and small Ichneumonids, it is best to prepare a few specimens by each method.

5. **Microcryptus basizonius,** Grav. **var. curtulus,** Kr.

M. basizonius is one of the commonest and most widely known parasites of *Diprion* species in Europe, although it has not been recorded from *Diprion polytomum.* Previous records of its European distribution and hosts are given below :—

Diprion frutetorum, F. ...	(Russia, Meier, 1927).
D. pallidum, Kl.	(Finland, Forsius, 1911).
D. pini, L.	(France, De Gaulle, 1919 ; Russia, Meier, 1927 ; Germany, Schutze and Roman, 1931 ; Poland, Sitowski, 1925–29 ; Holland, de Fluiter, 1932).
D. sertifer, Geoff. ...	(Russia, Meier, 1927 ; Poland, Sitowski, 1925).
D. similis, Htg.	(Finland, Forsius, 1911).
Banchus femoralis, Thoms.	(Germany, Habermehl, 1924, as hyper. ; also Scheidter, 1934).

So far only var. *curtulus* has been bred from *D. polytomum* cocoons in Europe, but *basizonius* has been found to attack *D. polytomum* very readily in the laboratory in England and in the field in Canada. As with all the cocoon parasites it is by no means easy to assess the true value of this parasite from the small samples of host cocoons it has been possible to collect. It is widely distributed in Czechoslovakia, from the lowest localities in mid-Bohemia to the heights of the Riesengebirge, and has been present in practically all the samples taken. It has never reached very high numbers, usually from 3 to 7 per cent., which figures certainly underestimate the total losses due to this parasite. Since, in biology and distribution, *basizonius* and var. *curtulus* have been found identical, it is perhaps permissible to consider the part played by the former as a controlling agent of the Pine Sawflies, which have been studied in large numbers, as an index of the value of this species. More especially from the practical point of view, since *M. basizonius* is the species imported into Canada in by far the greatest quantity, it is important to realise its possibilities. As a parasite of *D. sertifer* in the Riesengebirge Mountains it has been found parasitizing from 30 to 80 per cent. of the cocoons in different years. On the same host in Hungary its frequency varies from 10 to 52 per cent. in different localities and on different occasions. In the very extensive infestation in Sweden it accounted for 17·5 per cent. of overwintering cocoons in 1935, and 40 per cent. in 1936, by the end of which year the infestation had died down. On this host then, it forms a very considerable proportion of the parasite complex, which undoubtedly plays a major part in controlling this forest pest. On *D. pini* we have not the same amount of experience (27 million *D. sertifer* were collected in the past three years), but reliable records indicate the importance of *M. basizonius* on this host also. Recently, in Holland, de Fluiter (1932) records it parasitizing 36·5 per cent. of *D. pini* cocoons, and in Poland, Sitowski found it reaching 90 per cent. parasitism of the same host and considered that *M. basizonius* alone was responsible for reducing certain outbreaks of the Pine Sawfly.

The female of *M. basizonius* var. *curtulus* can be easily distinguished from the other parasites of *D. polytomum* by the following characters :—The pentagonal areolet of the forewing ; the reddish colour of the post petiole and segments 2, 3, and 4 of the abdomen, and the white speck on segment 7 ; and the white-banded antennae. The male is more slender than the female but has a similar pentagonal areolet and reddish abdomen, although the white area on segment 7 is much smaller. In the male the antennae are entirely black. Average length of male 6–7 mm. ; of female, 7–8 mm. Var. *curtulus* can be distinguished from *basizonius* by the absence of the white base to the hind tibiae, which is a marked character of the latter species; by the abdominal segments, the first being weakly longitudinally striated, the second very weakly punctate, centrally basally the punctation closer and tending to be arranged in longitudinal striae. They both have filiform antennae, with the postannellus longer than the scape, thorax entirely black, and metathoracic spiracles small and subcircular.

This is a primary parasite of *D. polytomum*, ovipositing in the cocoon, in which takes place the whole of the larval development, the prepupa or pupa of the host being destroyed. Mating, which has been observed in the laboratory, takes place very soon after emergence. The male generally approaches the female from the front, strokes her antennae, then quickly mounts her and holds her in the mesopleural region with his front claws. The abdomen of the male is then flexed sideways and under the exserted ovipositor of the female to allow the insertion of the penis. After copulation, which usually occupies about half a minute, the female remains motionless for a short time and then proceeds to inspect the cocoons prior to oviposition. She first senses their shape by applying the surface of her antennae to them, then flexes the abdomen and bores with a slight circular motion through the hard integument. The sheath is now thrown free and the ovipositor works rapidly in and out of the aperture, as if stinging the host and testing its surface for egg-laying.

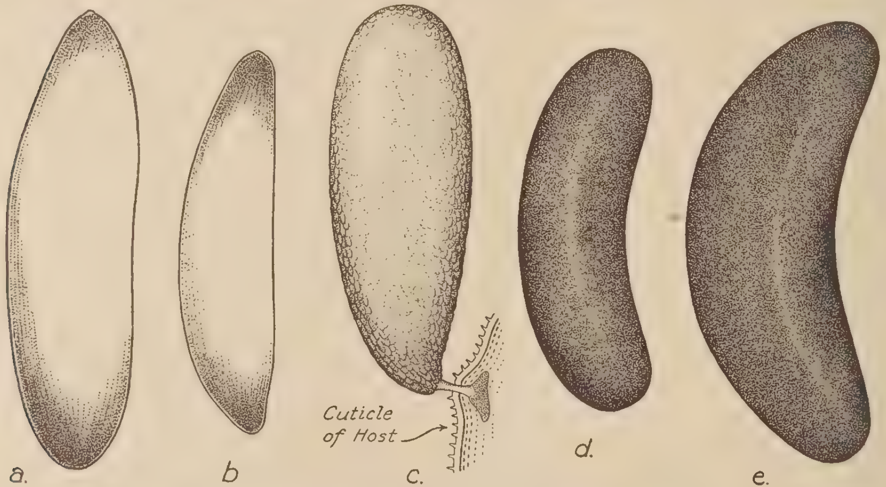


Fig. 1. Eggs of: (*a*) *Microcryptus basizonius* (× 45); (*b*) *Hemiteles areator* (× 45); (*c*) *Exenterus tricolor* (× 100); (*d*) *Holocremnus ratzeburgi* (× 75); (*e*) *Lamachus* sp. (× 75).

After a period of two or three minutes the ovipositor is slowly withdrawn and the egg is seen flowing down it. In one observation, during which the side of the cocoon was removed, the egg was seen emerging and swelling suddenly, the chorion hardening, leaving the egg lightly attached to the thoracic pleural region of the host. In many cases the egg was laid on the body in various positions without attachment. Females emerging from field collected cocoons at the normal time paralyse the host and render it inactive, but in laboratory-bred individuals this power of paralysing appears to get successively weaker and weaker, until ultimately very few of the prepupae are affected by the sting of the parasite. This will often result in the eggs being crushed by the active prepupa. Under laboratory conditions the parasite appears to be unable to distinguish between parasitized and unparasitized cocoons, since cocoons with two and three eggs were found in the rearing cages nearly as frequently as those with single eggs, although a fair supply of hosts was always present. From one cocoon a maximum of twelve eggs was obtained, but this number occurred when two females were together in the same cage. As only one individual can arrive at maturity in one host, the laying of superfluous eggs in the same cocoon constitutes a distinct loss to the population. Under natural conditions, however, where the host material is more abundant and the range of the parasite so very much greater, this overlapping should be very infrequent. At laboratory temperatures (15–19°C.) the egg hatches in from three to four days after oviposition.

The egg (fig. 1*a*) is white in colour and opaque, somewhat sub-reniform in shape with one end tapering more acutely towards the micropyle, a tiny projecting knob. Conspicuous longitudinal striae are present on the chorion and its surface is dull, not shining. The average length of the egg is 1·3 mm. and average maximum breadth 0·35 mm.

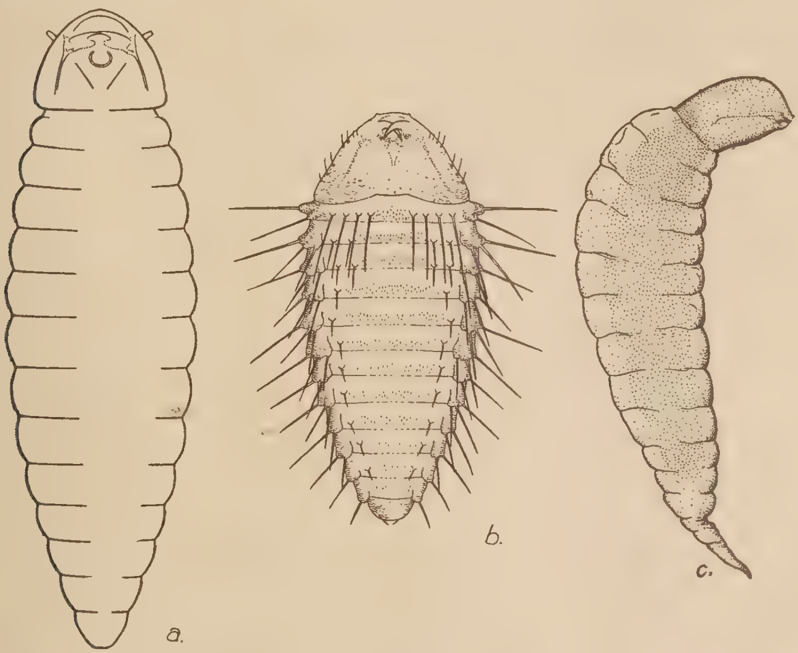


Fig. 2. Primary larvae of (*a*) *Microcryptus basizonius* (× 60) ; (*b*) *Exenterus tricolor* (× 100) ; (*c*) *Holocremnus ratzeburgi* (× 75).

On hatching, the primary larva is white in colour, the body surface being dull and the head glistening. It is fusiform in shape (fig. 2*a*) and consists of a head and 13 body segments, the apical segment being conical and slightly indented. The head is characterized chiefly by a pair of conspicuous antennae, a pair of curved mandibles and a fairly well chitinized internal skeleton, while the skin of the body is covered with small triangular-shaped spinules. The mouth-parts and supporting skeleton (fig. 3) are similar in outline to those of the mature larva, except that the mandibles are curved (straight in four succeeding instars) and less strongly chitinized, the labial struts are absent and do not appear until the second stadium, and the labial and maxillary sensory papillae are represented only by tiny dots. In length the newly-hatched larva measures 1·44 mm. by 0·36 mm. in breadth at the middle. When actively feeding, the larva throughout its five stages is dark greyish-green in colour, except for the head, first three and tenth segments, which are whitish. At the end of the feeding stage this green colour gives place to a dark creamy-white.

The larvae of *Microcryptus* during development pass through five stadia. At room temperatures (15–19°C.) and humidity (50 per cent. R.H.) the length of time passed in the first stage is two to three days; in the second, two to three days; in the third, three days; in the fourth, three days; and in the fifth, up to the end of feeding, three days. When the mature larva has finished feeding it begins to spin its cocoon (this marks the beginning of the prepupal stage), which it completes in from three to four days. A further twelve to thirteen days are spent within the cocoon in the prepupal and pupal stages, and the fully-formed adult emerges 33 days after the egg has been laid. In the constant temperature and humidity room, where the temperature is much higher (22°C. and 70 per cent. R.H.) these times are shortened and the entire life-cycle is completed in 24 days.

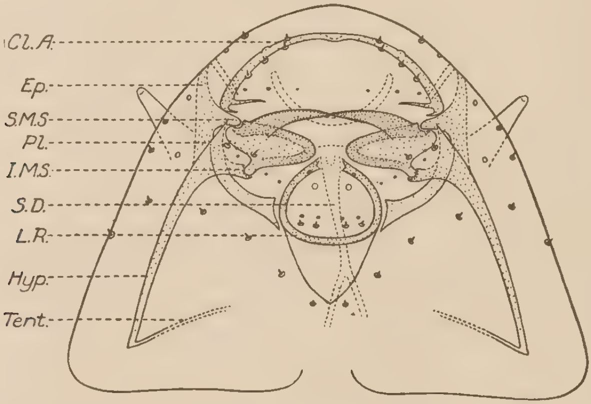


Fig. 3. Head of primary larva of *Microcryptus basizonius* (× 150): *Cl.A*, clypeal arch; *Ep*, epistoma; *Hyp*, hypostoma; *I.M.S*, inferior mandibular strut; *L.R*, labial ring; *Pl*, pleurostoma; *S.D*, salivary duct; *S.M.S*, superior mandibular strut; *Tent*, tentorium.

In Bohemia *Microcryptus* passes through at least two, or more usually three, generations in the year in cocoons of *D. polytomum*. The parasites that overwinter as prepupae pupate and emerge early in spring, in April or May, before the sawfly host emerges, and immediately oviposit in unparasitized cocoons of the same generation. The second generation of adult parasites emerges early in July, at the time when cocoons of the first generation of *D. polytomum* are formed, and immediately commences oviposition. The third generation of parasites emerges in September and oviposits on the second generation cocoons of the host, in which hibernation of the parasite prepupae takes place. On *D. sertifer* in Bohemia there are also three generations, but on the same host in Hungary, four generations may be passed in the year. Here the spring is earlier, autumn is mild and late, and the summer temperature high, so that there is a longer active period and the parasite's life-cycle is shortened. Also, in the case of this host, cocoons are available through the whole summer.

The mature larva (fig. 4*a*), which measures 9 mm. in length by 4 mm. in breadth at the middle, is somewhat cylindrical in shape with both ends tapering narrowly. The ventral side is flattened and the dorsal strongly convex. It consists of a head with strongly chitinized mouth-parts and supporting skeleton and 13 body segments. Dorsally, in segments 4 to 10, there are conspicuous curved transverse swellings, while in segments 4 to 11 hypopleural lobes are present. Ventrally on each of the first three segments, a pair of small papillae (vestigial legs) can be distinguished. The cuticle of the body, which is slightly shiny, is covered with small spinules, while the cuticle of the head is very shiny and glabrous. Under the high power of the microscope the skin armature (fig. 16*a*) can be seen to consist of fairly regular rows of small, bluntly pointed, conical scales or spinules, with wide, rounded bases. They measure 0·01 mm. in height and are approximately the same width at the base, being purely cuticular structures. There are also occasional sharp, strong microsetae, 0·02 mm. long, scattered over the body segments. These are articulate, trichoid, and probably hypodermal in origin. The tracheal system is of the usual Ichneumonid type, with accessory thoracic branches to the longitudinal trunks and nine pairs of spiracles. The spiracles (fig. 15*a*) are fairly large and well chitinized, and consist of three distinct parts, an atrium, a short connecting stalk, and a closing apparatus. The atrium is very broadly pear-shaped, the flattened, broader end bearing the very small external opening, the lower, narrower end joining the stalk. It has rather irregular annular thickenings to the sides, and is 0·035 mm. broad. The short, annulated stalk is 0·018 mm. wide, and leads into the closing apparatus with much thickened walls and a narrow central meatus. This leads into the trachea. The whole spiracle is 0·075 mm. long.

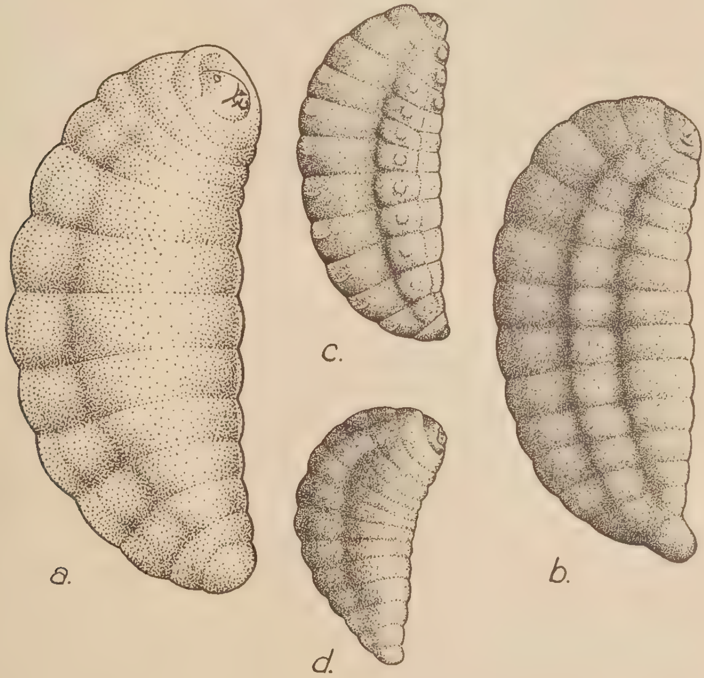


Fig. 4. Mature larvae of (*a*) *Microcryptus basizonius* (× 10); (*b*) *Holocremnus ratzeburgi* (× 9); (*c*) *Exenterus tricolor* (× 7); (*d*) *Hemiteles areator* (× 6).

The chief features of the head are the strongly chitinized mouth-parts and supporting skeleton, which stand out very clearly through the cuticle; the dorso-anterior epicranial lobes, which are clearly demarked by the metopic suture; the temporal fossae, which are darkened vertical areas, one on each side of the epicranial lobe just above the antennae; the antennae, which are small but have large conspicuous concentrically ringed bases; and the triangular area above the clypeus, clearly marked off by the frontal sutures. The mouth-parts consist of clypeus, labrum, mandibles, maxillae, labium, salivary duct, ligula, and maxillary and labial palps or sensory processes. On the upper margin of the colourless clypeus there is a strongly chitinized transverse arch, the clypeal arch. This arch is not present in all Ichneumonid larvae, but appears to be a fairly constant feature of the Cryptines, in many cases affording a useful distinctive character. On each side of the clypeus, close to the clypeal arch, there are three setae and a pair of sensillae. Two further pairs of sensillae are present on the thin and colourless labrum. The mandibles, which are strongly developed on a sub-quadrate base, are provided with two rows of fairly strong bristles. Two slight unchitinized swellings beneath the mandibles constitute the maxillae. Each bears a maxillary palp and three pairs of setae. The maxillary palp is made up of a pair of sensory pits, the inner circular and the outer semi-circular, both of which are enclosed and surrounded by a lightly pigmented chitinous ring, the whole process being slightly raised. This structure gives the palpi a figure 8 appearance under low magnification. The cuticle of the maxilla is attached laterally to a thin inward projection of the maxillary strut. Between and below the maxillae is the colourless labial area, marked out by the labial ring. It bears a pair of processes similar to those on the maxillae—the labial palps. Below these are two pairs of strong setae. The opening of the salivary duct is situated between the two upper ends of the labial ring just below the mouth opening. It is strongly chitinized and bears a pair of sensillae. Underneath is the lightly chitinized ligula. The chief structures of the supporting skeleton are the superior and inferior mandibular struts, the pleurostoma, epistoma, hypostoma, maxillary struts, labial struts, labial ring, clypeal arch, and tentorium. The mandibles articulate on the superior and inferior mandibular struts by means of a ball and socket joint. In the lower articulation a condyle on the mandible articulates in a fossa on the inferior mandibular strut, while in the upper this order is reversed, the condyle being on the strut and the fossa on the mandible. The two mandibular struts are joined together on each side by the pleurostoma, which continues above the clypeus as the epistoma. This latter forms a discontinuous arch to which the thin anterior arms of the tentorium are attached. On its surface the epistoma bears three pairs of setae. The inferior mandibular strut is continued latero-ventrally, as the hypostoma, to join up with the internal posterior arms of the tentorium. About one-quarter along its length, the hypostoma sends off the maxillary strut into the maxilla. The labial area is defined by the incomplete U-shaped labial strut. The only other chitinized structure present in an external view of the face is the darkened floor of

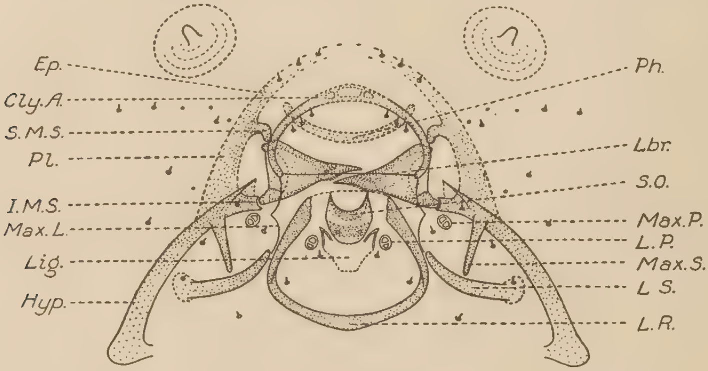


Fig. 5. Mouth-parts of mature larva of *Microcryptus basizonius* (× 60) ; *Cly.A*, clypeal arch ; *Ep*, epistoma ; *Hyp*, hypostoma ; *I.M.S*, inferior mandibular strut ; *Lbr*, labrum ; *Lig*, ligula ; *L.P*, labial palp ; *L.R*, labial ring ; *L.S*, labial strut ; *Max.L*, maxillary lobe ; *Max.P*, maxillary palp ; *Max.S*, maxillary strut ; *Ph*, floor of pharynx ; *Pl*, pleurostoma ; *S.M.S*, superior mandibular strut ; *S.O*, salivary opening.

the pharynx which, on focussing down under the microscope, appears as an inverted arch. In addition to the setae, already mentioned, there are two further groups outside the main skeletal system, a group of three on each side of the lower part of the pleurostoma, and one of six higher up in this area and external to the superior mandibular struts.

The liberation of this valuable parasite in Canada was advised from the very first. In 1933, 397 individuals of *M. basizonius* were liberated, a large number of which had been bred throughout the winter in the laboratory at Farnham Royal, most of the remainder coming from a *D. sertifer* infestation in the Riesengebirge. In 1934, 63,000 individuals were liberated, having been collected from big infestations of *D. sertifer* in the Riesengebirge and in Hungary. In 1935, 64,000 were liberated, the majority from the same host from Sweden and Hungary, but a small proportion of these, probably not more than 2,000, being the var. *curtulus* from *D. polytomum* in Bohemia. In 1936, 3,483 specimens were liberated, half of which were var. *curtulus* from *D. polytomum*, the remainder from *D. sertifer* from Sweden and Hungary. Thus a total of 131,205 parasites has now been liberated. The true *M. basizonius* had established itself in the Canadian infestations by 1935, when it was recovered from *D. polytomum* cocoons there. With this encouraging start there is every reason to hope that *M. basizonius* may eventually prove as effective a check on *D. polytomum* in Canada as it is on the other *Diprion* species in Europe. In considering the chances of its success, one important point must be remembered. In Canada quite a large proportion of the sawfly prepupae go into diapause every year, remaining in the cocoons for 2, 3, or even 4 years. This ensures a constant and plentiful supply of hosts, and, as has been pointed out, this cocoon parasite can develop three or even four generations in the year to the host's two. This results in a quicker reproductive rate on the part of the parasite, making the chances of its overtaking the host and eventually controlling it very much greater.

6. **Leptocryptus aereus,** Grav.

Previous records of this species show that it has often been bred from Lepidoptera, in many cases being definitely quoted as secondary. During the investigations it has turned up occasionally in batches of *D. polytomum* cocoons from different regions in Bohemia, though never in numbers. It occurred in greatest abundance at Kout in the Böhmerwald in 1934, when 8 per cent. of the cocoons produced this species. At the same time the total parasitism was high—67 per cent. Since then it has never appeared in more than 1 or 2 per cent., mainly from the Böhmerwald and South Bohemia.

This small, neat species is fairly easy to recognise by its size alone, never exceeding 5 mm. in length, usually much less, with slender, long-petiolate abdomen, large wings, and long, curved antennae. Head and thorax black and abdomen almost entirely red, except for the petiole, which is black with a red spot centrally posteriorly, and segments 2 and 3, which are black antero-laterally. Metathorax heavily punctate, with areolation present, but weakly developed. Areole pentagonal with outer side missing. Ovipositor short, 0·8 mm., or approximately one-third the length of the abdomen.

L. aereus is hyperparasitic upon various parasites of *D. polytomum*. It has been found destroying the larvae of *Exenterus*, *Holocremnus*, and *Lamachus*, and may attack others. It is possible that it will act as a primary upon the sawfly, but this has not yet been found in examining cocoon remains, and laboratory experiments have failed to demonstrate this. Two or three eggs are usually laid through the cocoon when the primary parasite is fairly well developed. In more than half the cases observed two parasites have succeeded in reaching maturity and emerging.

It is hardly necessary to point out the danger of such a confirmed hyperparasite in Canada.

7. **Spilocryptus abbreviator**, F.

This parasite has been bred from a few Lepidopterous hosts in Great Britain. We have no records from the Continent, and none from Hymenoptera. During the present work it was obtained very occasionally from the cocoons of *D. polytomum* from the lower-lying localities in Bohemia, especially in the Brdy Wald Region. In 1936 it was present in 3 per cent. of cocoons from that region, and in 5 per cent. of cocoons from Hradec in Silesia, from which locality the variety *hopei*, Grav., was obtained at the same time.

This is the only parasite of *D. polytomum* with short, rudimentary wings, otherwise it resembles very closely *Microcryptus*, and there is no danger of confusing it with the various species of *Gelis*, which have no wings at all. The following characters are sufficient to recognise it among the Cryptines : Head and thorax black, occasionally scutellum red. Abdomen reddish yellow, with the last three segments black above, the last segment tipped with white. Antennae three-coloured ; basal portion (nearly half) reddish, middle four segments white, distal portion dark brown. The rudimentary wings just reach to the end of the metathorax but not as far as the petiole. The posterior femora are distally brown, posterior tibiae apically dirty white. Only females are known. Specimens from *D. polytomum* varied from 3·5 to 6·0 mm. in length, with the ovipositor two-thirds the length of the abdomen.

This species has been found attacking *D. polytomum* always as a primary parasite, laying its egg in the cocoon, the larva feeding externally on the prepupa, which is rarely completely eaten because of the rather small size of this parasite.

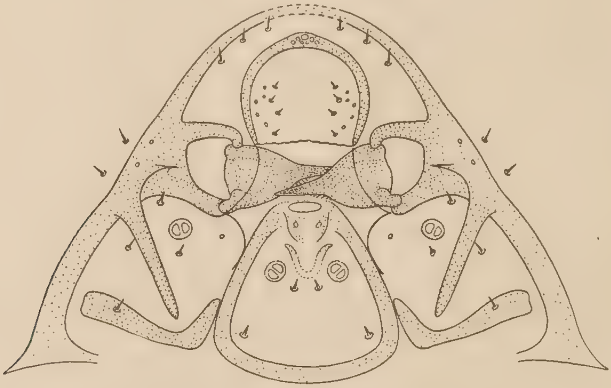


Fig. 6. Mouth-parts of mature larva of *Spilocryptus abbreviator* (× 107).

In its larval stages this parasite is fairly easily distinguishable from the other parasites, although the head skeleton and skin armature resemble closely those of the other Cryptines. The head skeleton (fig. 6), however, has one very marked feature distinguishing this species, that is the horseshoe-shaped clypeal arch, very distinct from the broad, flattened structure of the others. Again, the epistoma is almost complete, much more so than in *Hemiteles* or *Microcryptus*. The labial struts are distinctly angled where they join the labial ring. The region round the salivary opening is distinctly, though not heavily, chitinized. The ligula is distinctly visible as a small, wide-spreading U. The skin of *Spilocryptus* (fig. 16*b*) is covered with regular rows of sharply conical spinules, from 0·015 to 0·12 mm. in height. These are much more sharply pointed and of narrower base than the strong, blunt spinules of *Microcryptus*, and stronger and longer than those of *Habrocryptus*. There are also sparsely scattered microsetae, 0·04 mm. in length. The spiracle (fig. 15*b*), 0·07 mm. long, is large and stumpy, the atrium globular, with a reticulate strengthening of the walls somewhat similar to the spiracle of *Exenterus*, quite unlike the other Cryptines. A short, broad, annulated stalk leads to the well developed, thick-walled closing apparatus.

In the few instances when this insect has been recovered from *D. polytomum* cocoons, it has always been a primary parasite and there is no reason to suppose of its being otherwise. In view of the Cryptine's ability to go through several generations to the host's two in Europe, it certainly seems worth introducing this, as well as the other Cryptines, into Canada, where the ever-present supply of cocoons makes this habit especially valuable. The insect seems to prefer a low locality, below 500 m., with warm, sunny climate and not heavy rainfall.

8. **Habrocryptus polytomi,** Tschek.

The only previous record we can find of this insect is in Tschek's original description (Tschek, 1872), when it was bred from *D. polytomum* in Austria. It has occasionally turned up in Bohemia, bred from cocoons collected from spruce branches, but has never been abundant, at the most in 2 per cent. of the cocoons. It has always appeared in the lower and warmer localities, such as Dobřiš, the Sazava River region, and the lower parts of South Bohemia, Neu Bistritz, and Pleše.

The adult insect is easy to recognise, having the typically Cryptine features of a fine, right-angled petiole and large pentagonal areolet, together with a plain black head, thorax, and abdomen. It is most easily confused with *Hemiteles sordipes*, from which it may be distinguished by the absence of metathoracic areolation, by the white spot on the middle segments of the black antennae, and the areole being closed or, at most, with the outer side very faint or missing on one side, never entirely open on both sides. The black body is slightly polished, having very fine punctation. The second abdominal segment is edged with pale brown. The antennae are black, with the middle two or three segments white above only, not with a complete white ring. Legs dark reddish-brown, hind tibiae almost black. The metathoracic areolation is entirely wanting. Spiracles small and round. Length, 5 mm. Ovipositor half the length of the abdomen, or 1·5 mm.

In all the cases observed this has been a primary parasite of *D. polytomum*, laying its eggs in the cocoon and the larvae feeding externally on the sawfly prepupae or, occasionally, pupae.

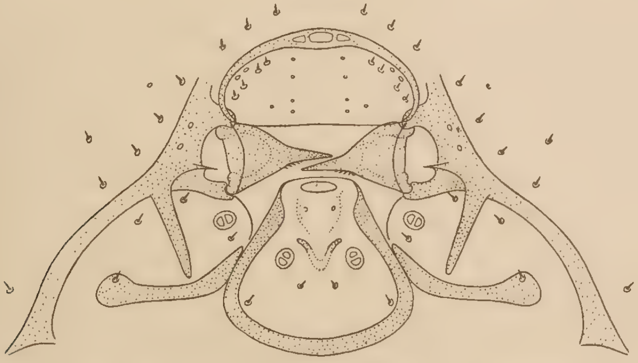


Fig. 7. Mouth-parts of mature larva of *Habrocryptus polytomi* (× 107).

The larva is very similar to those of the other Cryptines and can only be separated on microscopic distinctions. The general outlay of the larval head skeleton (fig. 7) is essentially similar to that of *Microcryptus* or *Hemiteles*. From both it can be distinguished by the very weakly developed epistoma and the arrangement of setae and sensillae on the labrum. It differs from *Microcryptus* in not having the strongly chitinized salivary opening and in the smaller and differently shaped ligula; from *Hemiteles* in the smaller, more chitinized ligula, V-shaped rather than Y-shaped, and in the structure of the clypeal arch. The chitinized floor of the pharynx can be seen in preparations, but is not included in the drawing for the sake of simplicity. The skin structure (fig. 16*c*) is quite distinct from that of either of the above species, resembling very closely *Spilocryptus*, but with shorter, weaker spinules, never more than 0·015 mm. long and more likely to be bent and twisted. There are occasional microsetae, 0·025 mm. long. The spiracle (fig. 15*c*) is quite distinctive, rather short, less than 0·07 mm. long over all, with the atrium shaped like a Chinese ginger jar, with a number of fine, annular thickenings, the stalk coarsely annulated, having the appearance of four globes end to end, and a small closing apparatus.

This is one of the least important parasites of *D. polytomum* in Europe, but, as it is undoubtedly a primary and probably monophagous, it would be worth making some experimental liberations in Canada in the heavily infested areas. From its distribution in Europe, a lowish altitude, not above 500 m., with a warm climate, would be most suitable.

9. **Hemiteles areator,** Panz.

This species has been recorded from at least twenty-eight different hosts, some of which are *Apanteles glomeratus*, *A. solitarius*, *Microcryptus basizonius*, *Meteorus versicolor*, *M. pulchricornis*, *M. ictericus*, *Diprion pini*, *Hemerobius stigma*, *Chrysopa nigricornis*, *Hyponomeuta padella*, etc. It has a wide distribution and is one of the commonest species of *Hemiteles*. In the course of the present investigations, this parasite has appeared regularly in samples of cocoons of *D. polytomum* collected from all over Bohemia. Although usually present in small numbers, only 1 to 5 per cent. of cocoons, it can occasionally attain a fairly high degree of parasitism; for example, 15 per cent. at Neu Bistritz in South Bohemia in 1934, and 10 per cent. in the Böhmerwald region in the same year. It has always been most abundant in the South Bohemian and Böhmerwald mountains, of regular occurrence but in small numbers in the low-lying, warm middle Bohemian areas, and absent from Silesia. It was bred from *D. sertifer* cocoons from the Riesengebirge Mountains in 1933 and 1934, where it was mainly hyperparasitic. Another species, *H. inimicus*, was far more prevalent as a hyperparasite on this host in the same locality.

This is the only Ichneumonid parasite of *D. polytomum* with dark markings on the wings. Among the HEMITELINI it may be distinguished by the following characters: Coloration rather variable, with head, thorax and abdomen black with a variable amount of brown-red markings; legs mainly red; ovipositor rather less than half the length of the abdomen; thorax with strong punctation, metathoracic areolation fully developed; wings with three dark bands; areolet regular, pentagonal, but with outer side missing. Length from 2·5 to 5·0 mm.

As can be seen from the host records, *H. areator* is frequently hyperparasitic. As is often the case with a Hymenopterous host, it can act either as a primary or secondary parasite on *D. polytomum*. In rather less than half the cases observed it has been primary on this host; in the majority of cases it has been hyperparasitic upon *Exenterus*, *Holocremnus*, *Lamachus* and *Microcryptus*. Eggs (fig. 1*b*) are laid in the host cocoon; the larvae feed externally on host or parasite.

The mouth-parts and supporting skeleton of the mature larva (fig. 8) are very similar to those of *Microcryptus basizonius*, but the two can be separated by the following distinctions: (1) By size, the area of the mouth-parts and skeleton in *Hemiteles* being only two-thirds as large as that of *Microcryptus*; (2) by the shape of the ligula; in *Hemiteles* this is shaped like a wide tuning-fork, in *Microcryptus* it consists mainly of two small triangular pieces underneath the chitinization of the salivary duct ; (3) by the chitinization of the salivary duct below its opening, this area being more weakly chitinized in *Hemiteles* than in *Microcryptus* ; (4) by the mandibles, those of *Hemiteles* being much more finely pointed than those of *Microcryptus* ; also the bristles on the mandibles of *Hemiteles* are small, whereas in *Microcryptus* they are large and conspicuous ; (5) by the zenith of the clypeal arch ; in *Hemiteles* this is broader and has greater areation than in *Microcryptus*. It is most likely to be confused with *Habrocryptus polytomi*, which it closely resembles in size and head skeleton. Points which distinguish it are the more complete epistoma of *Hemiteles*, the different structure of the clypeal arch, the Y-shaped, weakly chitinized ligula, and the arrangement of the sensillae on the labrum. The skin structure of *H. areator* (fig. 16*d*) is quite distinctive, consisting of a number of small, closely arranged papillae, at most 0·005 mm. high, with rounded, dome-shaped ends. These are quite unlike the sharp-pointed spinules of *Spilocryptus* or *Habrocryptus*, or the stronger, blunter ones of *Microcryptus*. There are sparsely scattered microsetae, 0·025 mm. long. The spiracles (fig. 15*d*) further serve to distinguish this from the other Cryptines. A regular, bluntly pear-shaped atrium has three annular thickenings, and surmounts a long, annular stalk, 0·045 mm. long, below which is a rather long, narrow closing apparatus. The whole spiracle is of a long and slender type, with an over-all length of 0·1 mm.

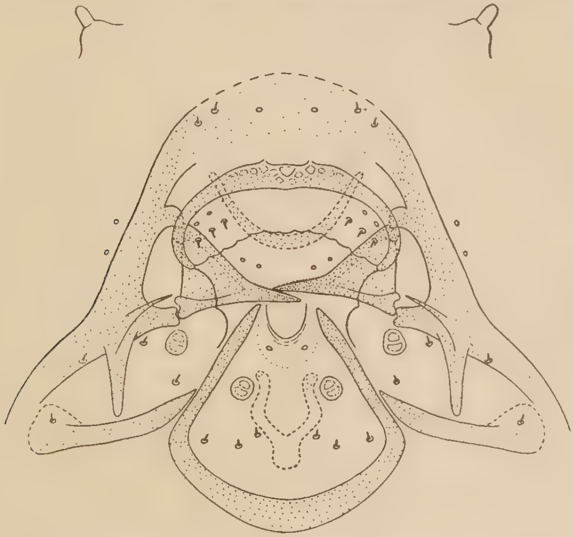


Fig. 8. Mouth-parts of mature larva of *Hemiteles areator* (× 107).

This species is so frequently hyperparasitic on the most important larval parasites of *D. polytomum* that its liberation in Canada, at the present state of our knowledge, is considered very inadvisable.

10. **Hemiteles sordipes,** Grav.

The only records of this species are as a hyperparasite and it has been recovered from *D. polytomum* cocoons on one or two occasions from the Brdy Wald area in mid-Bohemia, in every case as a secondary on the larval parasites *Exenterus* and *Lamachus*.

This species may be distinguished among the parasites of *D. polytomum* by the Hemiteline characters of the large, pentagonal areolet with the outer side wanting, and the complete areolation of the metathorax, together with its uniform, black coloration of the head, thorax and abdomen, only the legs being reddish. Further distinctions among the Hemitelines are afforded by the long, thinnish antennae; the ovipositor as long as the abdomen; the very good development of the lines dividing up the areolation on the metathorax; and the hyaline wings. Length, 4 mm.

It is unnecessary to describe the life-history or larvae of this hyperparasite, and needless to say, it should be withheld from liberation in Canada.

11. **Gelis acarorum**, L. (**Pezomachus acarorum**, L.) **and Gelis sp.**

There are only two previously recorded hosts of *G. acarorum*, in each case as a secondary, from *Microgaster tibialis*, Nees, and *Apanteles gracilipes*, Thoms. The majority of the members of this genus seem to be hyperparasitic. One or other of the species of *Gelis* are bred occasionally from *D. polytomum* cocoons collected in the field. It is never numerous, which is a good thing, as it is invariably hyperparasitic.

Both male and female are apterous, and cannot be confused with other parasites of *D. polytomum*.

12. **Delomerista sp.**

This genus, distinct from the true Pimplines (see characters given below), is at present in such disorder that it is impossible to assign to any species those examples bred from *D. polytomum*. It certainly does not belong to *D. pfankuchi*, Brauns, the only species undoubtedly recorded from pine sawflies (Sitowski, 1925; de Fluiter, 1932). It has been bred from cocoons from only two localities, in the Böhmerwald and in South Bohemia, in 1934, and has not been seen again since. In the Böhmerwald it was found in 4 per cent. of the cocoons examined.

This species can be distinguished from the other parasites by the sessile abdomen, black coloration of the body and the long ovipositor (at least half the length of the abdomen). It can be separated from the true Pimplines and other *Delomerista* spp. on the following characters: The metathorax has the central areolation very distinctly developed, the area superomedia and area posteromedia being completely enclosed. The area basalis is hardly recognisable and the side fields are not marked off. Head and antennae entirely black. Thorax black and polished, with puncturing and hairing, except on metathorax, very weak. Abdomen black, more strongly punctured, giving a less shiny appearance. The fourth, fifth, sixth and seventh, and sometimes third, abdominal segments have dull, dirty-yellow hind margins. The first two pairs of legs are entirely reddish yellow; hind legs of the same colour, except the tibiae (brown, white basally), and tarsi brown. Length from 6 to 8 mm. Ovipositor from 2 to 2·5 mm. long.

This is a primary parasite of *D. polytomum*, laying its eggs through the cocoon on the prepupa or pupa, upon which the larvae feed externally. The mature larva does not spin any cocoon, but remains through the prepupal and pupal periods naked in the host cocoon. This affords one means of separating *Delomerista* and *Pimpla* larvae and pupae from those of all the other Ichneumonid parasites. Further than this the larval skin structure and mouth-parts make the immature stages of *Delomerista* quite unmistakable.

The structure of the mouth-parts and supporting skeleton (fig. 9) exhibit only certain of the true Pimpline characters, together with some features typical of the CRYPTINAE. This is especially interesting in view of the way these two groups merge one with another in adult morphology. The Pimpline characters lie in the labial ring, very much thickened basally, the much reduced labial struts, and the shape of the mandibles, with long, strong teeth, bristly on the interior aspect only, and with broadly rounded bases. It differs from *P. alternans* in the full development of the hypostoma, the incomplete or weakly developed epistoma, the presence of a well developed clypeal arch and the absence of a spiny armature at the base of the pharyngeal opening. The presence of a clypeal arch is a typical Cryptine character, as is also the incomplete epistoma. The skin structure of *Delomerista* (fig. 16*e*) affords an easy means of identifying the larvae. In the first place it is the only larva, apart from *Monodontomerus* among the Chalcids, that is hairy. The hairs (macrosetae) are neither very close nor very long (0·1 mm. in length) compared with those of *Monodontomerus*, yet they are sufficient to give the larvae a hairy appearance without the aid of a microscope. Microscopically the skin is covered with quite large (0·01 mm. diam.) dome-shaped papillae, regularly spaced and not very close together. The spiracle (fig. 15*f*) is small and very simple, consisting of a perfectly plain, round atrium, 0·02 mm. in diameter, a straight narrow, annulated stalk, and normal type of closing apparatus above the trachea. The combination of these characters makes this a very easy larva to recognise.

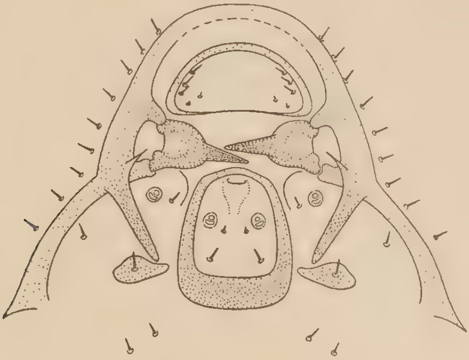


Fig. 9. Mouth-parts of mature larva of *Delomerista* sp. (× 107).

In view of the primary nature of this parasite and the fact that it can attain appreciable parasitism on *D. polytomum* in Europe, despite its rare appearance, it is certainly worth making experimental liberations of this species in Canada on the chance that it may find a set of conditions more suitable for increase. Judging by its limited appearance in Bohemia, it is partial to wooded, hilly country of not too great an altitude, between 400 and 600 metres, and with a moderate annual rainfall of about 500 mm.

13. **Pimpla (Itoplectis) alternans,** Grav.

This decidedly polyphagous parasite has been recorded from a variety of insect hosts, mainly Lepidoptera. There are two records from pine sawflies, both from *D. pini*, in France (de Gaulle, 1919) and Germany (Scheidter, 1934). During the present work this species and a variety, *kolthoffi*, Aur., were found fairly frequently parasitising *D. sertifer* in the Riesengebirge in 1933 and 1934. It has only occurred on *D. polytomum* in one locality and in one season, at Hradec in Silesia in 1936, when it was present in approximately 2 per cent. of cocoons collected from the ground. As with most other parasites of the cocoon stage, this paucity of records is misleading, in view of the small number of cocoons collected in previous years. Only in 1935 and 1936 were large numbers of cocoons collected which had had a reasonable exposure to natural attack by parasites. Many of the rarer parasites were found in these years.

This species may be distinguished from the other parasites of *D. polytomum* by the sessile abdomen, uniformly black coloration of head, thorax and abdomen, the absence of metathoracic areolation and the long ovipositor, approximately one-third of the length of the abdomen. It may be distinguished from the other Pimplines (being set aside by Thomson in a separate genus, *Itoplectis*) by the following characters : The groove before the mesepimeron is not angled opposite the punctiform fovea ; the last joint of the hind tarsi is distally longer than the second ; the thorax is polished and with only a very light covering of hairs, which by no means obscure the colour ; the fore legs are a bright reddish-yellow to yellow ; the hind tibiae three-coloured, with three dark brown rings, a broad one at base, a narrower one before the middle and one at the apex, white between the basal and middle ring, red between the middle and apical. Length, 7 mm. Ovipositor, 1·5 mm.

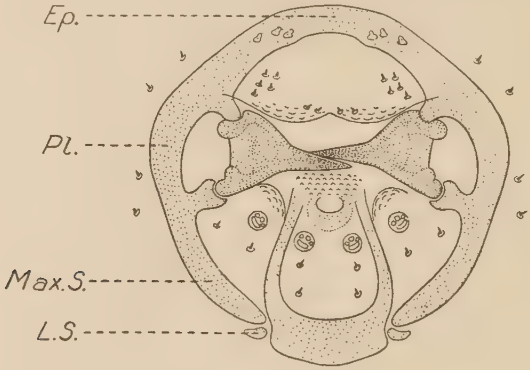


Fig. 10. Mouth-parts of mature larva of *Pimpla alternans* (× 107) : *Ep*, epistoma ; *L.S*, labial strut ; *Max.S*, maxillary strut ; *Pl*, pleurostoma.

In the cases that have come under our own observation, in both *D. sertifer* and *D. polytomum*, this is a primary parasite. It oviposits on prepupae or pupae within the host cocoon and the larva feeds externally. On the completion of feeding the mature larva does not spin any sort of cocoon, but enters the resting period naked in the host cocoon. In this way the mature larvae and pupae of this insect and of *Delomerista* can be distinguished from those of all the other Ichneumonine parasites of *D. polytomum*, which invariably spin a thin, papery cocoon within the host cocoon, in which the prepupae and pupae rest.

The larval mouth-parts (fig. 10) are very characteristic and at once set this aside from all the other parasites. The hypostoma is entirely wanting, and the epistoma, pleurostoma, and maxillary struts form an almost complete ring, broken at the bottom to admit the labial ring. This is of characteristic Pimpline form, strong, and with broad, thickened and rather flattened basal segment. The labial struts are reduced to mere vestiges, this being another Pimpline characteristic. The mandibles are strong and coarse, the inner aspect of the heavy, pointed teeth being armed with bristles. The labrum and maxillary lobes are covered with small, round projections giving them a warty appearance. The labium is armed with a close array of small, sharp, triangular teeth. The labial and maxillary palps have not the appearance common to those of the other Ichneumonines. Instead of two large pits surrounded by a pigmented ring, giving a figure 8 appearance, there are three or four small pits on the inner aspect (nearest the mouth) and one large curved pit outside these. The whole group is surrounded by a pigmented chitinous ring. In general, the head-capsule of the *P. alternans* larva is strong and well chitinized, and the mouth-parts very strongly chitinized, making them stand out conspicuously. The skin armature (fig. 16*f*) is peculiar to this species, consisting of small conical scales, equilaterally triangular in longitudinal section, not very thickly but regularly distributed. Besides these there are occasional small setae, never more than 0·03 mm. in length. The spiracles (fig. 15*e*) are absolutely characteristic, distinctly larger than in any other of the larvae, with a short, very broad stalk joining direct on to the trachea, without the intervention of a closing apparatus as in the other spiracles described. The atrium is a large, rather flattened sphere 0·045 mm. in diameter, with a very small external opening, less than 0·015 mm. in diameter. The inner wall of the atrium is lined with a number of short projecting processes all radiating towards the centre of the sphere. The stalk of the spiracle is formed of one ring and a large pear-shaped vessel, the lower end of which is divided by sutures into 6 petal-like components, which closely adhere together, clasping the end of the trachea.

This species has been found only as a primary parasite on the DIPRIONIDAE but there seem to be cases in which it acts as a hyperparasite among Lepidopterous hosts. This, however, should not be sufficient to condemn it as a sawfly parasite, and there are several good practical arguments for its introduction into Canada. In the first place, its extremely polyphagous habits make it peculiarly suitable for the two extreme ends of an infestation. In localities newly invaded by the sawfly, where it is not yet in sufficient numbers to maintain monophagous parasites, the more polyphagous species, such as *Pimpla alternans*, might be able to maintain themselves on a variety of hosts. As the sawfly increases in numbers, it would come in for more and more attention as a host. Thus, this is a particularly suitable species for use as a barrier against the spread of *D. polytomum*. Similarly, it would be able to maintain itself in cases of severely reduced populations of the sawfly, where the numbers of primary parasites would fall to negligible proportions. Another practical advantage possessed by this Pimpline is the possibility of obtaining it in really large numbers from one or other of its alternative hosts.

14. **Mesochorus thoracicus,** Grav., **M. fulgurans** Curt., **aud M. (?) dimidiatus,** Holmgr.

A great diversity of insect families is attacked both by *M. thoracicus* and *M. fulgurans*, which are two of the commonest members of the genus, with a wide distribution in Northern and Central Europe. *M. dimidiatus* is uncommon. The main host records for *M. thoracicus* are *Peronea maceana*, *Microgaster* sp., *Tachina* sp., *Tortrix viridana*, *Agelastica alni*, *Chrysomela varians*, and *Galleruca lineola*; for *M. fulgurans—Diprion pini*, *D. laricis*, *D. variegatus*, *Ceromasia inclusa*, *Trophocampa* sp., on *Abraxas grossulariata*, and *Eupithecia pimpinellaria*. The genus is thought by Sitowski (1925–29) to be entirely hyperparasitic and this is probably the case with *M. thoracicus* and *M. fulgurans*, so far as the records indicate, although an examination of the cocoon from which *M. thoracicus* emerged showed a trace of the larval skin of a primary parasite. Only one individual of each species was bred out. They emerged from first generation cocoons of *polytomum* collected as larvae in Tyssa, North Bohemia. Because of their rarity and comparatively unimportant status as probable hyperparasites, no data have been obtained on their biology.

The MESOCHORIDES can be recognised among the other Ophionine tribes by the conspicuously large rhomboidal areolet, strongly shining body, and the pair of elongate styloid appendages in the male. These characters will also separate them from the other parasites of *Diprion polytomum*, while the following colour table will separate them from each other.

	M. fulgurans	*M. thoracicus*	*M. dimidiatus*
Head	Light reddish-brown	Female black; male reddish-brown	Reddish-brown
Thorax	Reddish-brown	Reddish-brown, mesonotum flecked with black at middle, metanotum black	Black
Abdomen ...	Reddish-brown	Black, hinder edges white	Female, segment 1–2 or 3 black, with light edges, 4–7 reddish-brown; male black, segments 1 and 2 with light hind edge, 3 reddish-brown

Because of their hyperparasitic habits care should be taken not to liberate any of these species in Canada.

15. **Holocremnus ratzeburgi,** Tschek.

Members of the genus *Holocremnus* are mainly parasitic on TENTHREDINIDAE, but practically nothing has been written on the biology of *H. ratzeburgi*, and records of its occurrence are few. It has been recorded from :—

Bupalus piniarius ...	Germany (Habermehl, 1922).
Diprion pini	Russia (Meier, 1929); Germany (Scheidter, 1934).
Diprion polytomum ...	Finland (Forsius, 1932); Austria (Tschek, 1872).
Trichiosoma lucorum ...	Germany (Schmiedeknecht, 1908).
Microcryptus contractus ...	Poland (Sitowski, 1925).

This last record, in which Sitowski states that *H. ratzeburgi* is hyperparasitic on *M. contractus*, appears, from a consideration of certain facts in the life-history of both species, to be very unlikely. The egg of *Holocremnus* is laid in the host larva and it develops as an internal parasite inside the spun-up host, while that of *Microcryptus* is laid in the cocoon and it develops as an external parasite. It would therefore be much more likely for the external-feeding *Microcryptus* to destroy the internal-feeding *Holocremnus* than for the latter to destroy the former.

This is one of the three most important larval parasites of *D. polytomum* in Europe. It has invariably been present in every locality in which the sawfly has been collected throughout Bohemia and in Germany. Usually it is present in quite good numbers, from 7 to 20 per cent., contributing a very fair proportion of the parasitism. When in small numbers, 1 to 5 per cent., it is because the total parasitism is low or it has suffered from hyperparasites, or in competition with intrinsically superior parasites (usually cocoon parasites, especially Chalcids). In places where the sawfly host is present in regular numbers it attains its highest parasitism. For example, at Tyssa in 1932 and 1933 it reached 14 per cent. and 17 per cent.; in the Kunžak and Neu Bistritz areas of South Bohemia in 1932, 2 per cent., 1933, 4 per cent., 1934, 18 per cent., 1935, 20 per cent., 1936, 12 per cent. In the Böhmerwald, where there was a great abundance of the host in 1934, it reached 18 per cent., and in 1935 approximately the same figure. In the highest locality where *D. polytomum* has been found, the Riesengebirge Mountains at 800 metres, it reached 12·0 per cent., a high enough figure considering that parasitism in general was low in this region. Thus in regular abundance it equals *Exenterus* and surpasses *Lamachus*, though the latter has shown higher figures on occasions.

Superficially the adults can at once be recognised from the other parasites of *D. polytomum* by the uniform black matt coloration of the thorax and abdomen, unrelieved by any markings except the yellow tegulae. In contrast to the black body the immaculate red femora stand out conspicuously. The small, quadrate, stalked areolet of the forewing, although sometimes absent, is also distinctive. Of all the subgenera of the old genus *Limneria*, this is the most difficult to recognise, and is easily confused with *Angitia* parasitic on Lepidoptera. The female of *Holocremnus* may be recognised readily from the latter by the shorter ovipositor, never protruding beyond the anus ; the male can only be distinguished by the shape of the head and colour of the abdomen. Length averages 11·5 mm.

H. ratzeburgi is a primary parasite of *D. polytomum*, attacking the fourth and fifth stage larvae, the eggs being laid most usually in the last thoracic or first few abdominal segments, a black puncture mark remaining visible on the skin of the parasitized larva at the site of insertion of the parasite's ovipositor. There must be a backward movement of the parasite's eggs in the body cavity of the larva, as in dissected larvae the majority of eggs and all empty eggshells were found in the posterior abdominal segments. Only a few freshly-laid eggs were found in an anterior position and close to the puncture mark. Such a movement could easily be brought about by the peristalsis of the larval intestine which would tend to push the eggs gradually backwards in the body cavity. Very frequently two eggs are deposited in a larva, and as these are most usually found closely adhering in pairs, it seems likely that they have been laid by one female at the same time. The laying of the eggs does not seem to affect the host larva in the least ; it continues feeding and almost invariably enters the prepupal stage and spins its cocoon before succumbing to the parasite. There must be an interval, the duration of which is uncertain, perhaps one, two, or three weeks, between the laying and the hatching of the eggs to allow for this. Eggs laid in autumn on the second generation of *D. polytomum* invariably overwinter in the hibernating larva and hatch in the following spring. It is by no means unusual for eggs to remain unhatched and the parasitized larvae to recover. On one occasion, four unhatched *Holocremnus* were found in the body cavity of a healthy adult *D. polytomum*. They must have remained in the coelom

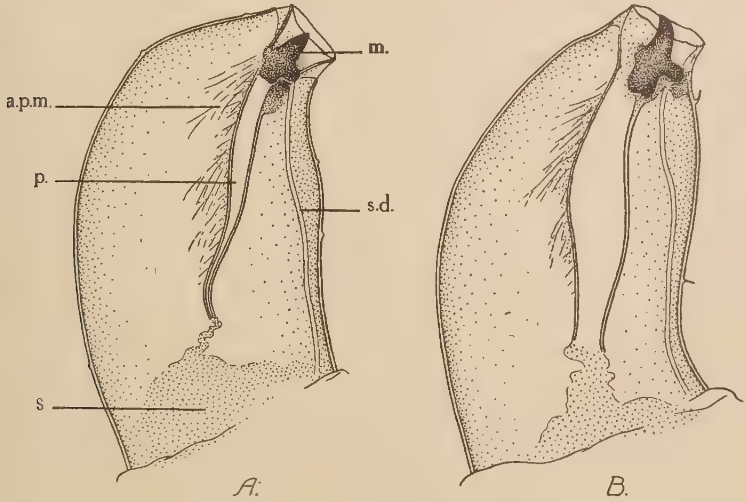


Fig. 11. Head of primary larva of (*A*) *Holocremnus ratzeburgi* ; (*B*) *Lamachus* sp. (both × 200) : *a.p.m*, anterior pharyngeal muscles ; *m*, mandible ; *p*, pharynx ; *s*, stomach ; *s.d*, salivary duct.

throughout the metamorphosis. On comparing parasitism figures based on dissections of larvae with the actual emergence of parasites from similar batches, the former figures were always found to be higher, the most extreme case being 28 per cent. by dissection and 14 per cent. by emergence for the second generation at Tyssa in 1932. The egg (fig. 1*d*) is sub-reniform in shape, from 0·68 to 0·8 mm. in length and 0·23 to 0·26 mm. in breadth, of a dark brown colour, with an exceedingly tough chorion, but showing no sculpturing or markings.

The primary larva (fig. 2*c*) is of typical caudiform shape, cylindrical, with a large strongly chitinized head-capsule, thirteen body segments and a comparatively short tail. After hatching it measures 0·9 mm. in length, the head being 0·27 mm. long and 0·14 mm. broad, and the tail 0·17 mm. long. The skin is uniformly smooth on the body and tail. The head (fig. 11*a*) has a pair of strong, hooked, sharp-pointed mandibles, set just within the buccal cavity, while the pharynx has thick chitinized walls and is strongly muscular for two-thirds of the length of the head. It then leads into the thin-walled stomach. The salivary duct opens into the base of the buccal cavity between the mandibles. There are two pairs of papillae ventrally and three pairs dorsally on the head-capsule. There are no antennae and nothing resembling maxillary or labial structures have been made out.

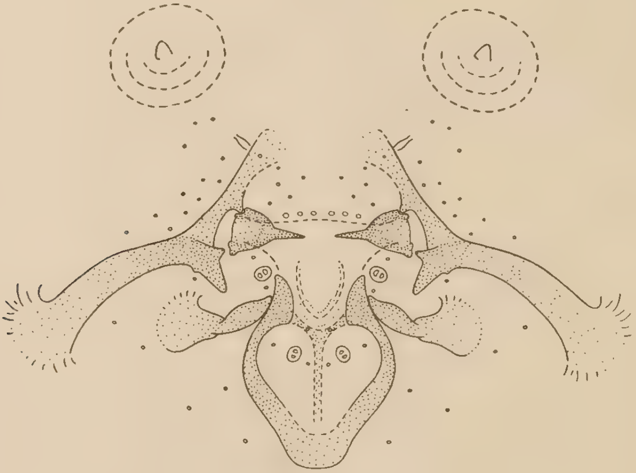


Fig. 12. Mouth-parts of mature larva of *Holocremnus ratzeburgi* (× 80)

The number of larval instars undergone has not been ascertained. At the first ecdysis the characteristic head-capsule and tail of the primary larva are lost. It continues to feed internally and in 8 to 12 days has reached maturity (fig. 4**b**), emerges from the now completely empty host skin, and spins a white, papery cocoon within that of the host. The very characteristic egg-shells are always present in the empty host skin. Pupation takes place in 4 to 5 days, and 2 or 3 days later the adult emerges. There are two generations in the year, corresponding with those of *D. polytomum*. Adults are on the wing in June and July, and again late in August and September. Eggs laid in September, in the second generation larvae of *D. polytomum*, do not hatch at once but remain in the hibernating host prepupa and hatch, and the larvae develop, in the following spring. Thus the length of larval and pupal life is much the same in both generations, being mainly affected by the prevailing temperature.

This being the only Campopleginine among the *D. polytomum* parasites, the larva, with the characteristic head-skeleton (fig. 12) of that group, is very easy to recognize. The most obvious features characterizing both this species and most of the group, and easily visible in the living larvae, are: the labial ring, the base of which is drawn out or produced ventrally, giving it almost a keyhole shape, distinct from the circular or horseshoe shape amongst the other parasites; the Y-shaped pigmented superficial area within the labial ring and below the salivary opening, dividing the labium into two distinct lobes; the greatly reduced maxillary struts and obtuse angle made by hypostoma to pleurostoma; the labial struts adjoining the upper sector of the labial ring, level with the salivary opening. Besides these there are a number of minor characters distinguishable in a microscopic preparation, the chief being: the incomplete epistoma; the mandibles with long, pointed teeth, sickle-shaped in lateral view, and without bristles; the U-shaped salivary opening; the large number and arrangement of sensillae. The skin structure of *Holocremnus* (fig. 16*h*) is not a very definite feature, nothing like that of the Cryptines or *Exenterus*. The skin is closely covered with small, rather flattened and rounded conical scales. They are less closely packed and more rounded than in the case of *Lamachus*. There are no hairs or setae on the larvae. The spiracles (fig. 15*h*), on the other hand, afford a ready distinction, being unlike those of any other group. They are minute, actually smaller than in the Chalcid parasites of this host, with a simple atrium 0·018 mm. in diameter, surmounting a slightly wider globular chamber, representing the stalk, which leads directly into the tracheal arm, which has to be constricted to receive it. There is no closing apparatus, but the stalk has a number of fine, hair-like processes radiating inwards from its walls. The whole spiracle has the shape of a cottage loaf, and is only just over 0·02 mm. in length. The small size, and absence of a closing apparatus, seem typical features of the spiracles of endoparasitic larvae, being prevalent throughout a number of such larvae that have been examined.

H. ratzeburgi, as one of the most important parasites of *D. polytomum* in Europe adaptable to a wide range of climatic conditions, should have the possibilities of becoming a useful controlling agent in Canada. Its liberation was advised in the first year of the investigation, since when 3,500 have been sent over and liberated in the infested areas, but so far as our information goes, this species has not yet become established under the new conditions.

16. Lamachus sp.

So far as is known, all eleven species of this genus confine themselves to the Diprionidae for hosts, but only one, *L. spectabilis*, Holmgr., has been recorded as attacking *D. polytomum*. The present species, very close to but distinct from *L. marginatus* of *D. pini*, is possibly new, but this cannot be determined without reference to Ratzeburg's original types and others in the museums in Germany.

This has been found to be one of the commonest larval parasites of *D. polytomum*, coming next to *Exenterus* and *Holocremnus* in abundance, occasionally surpassing both.. The normal abundance is from 4 to 10 per cent.; for example, in 1932 at Tyssa in the Erzegebirge Mountains, 4 per cent.; in the Brdy Wald, 12 per cent.; South Bohemia, 8 per cent.; Tharandt, in Saxony, 6 per cent.; and the Riesengebirge Mountains, 4 per cent. It is very rarely absent from a locality, though it has occasionally failed, and is usually scarce in the lowest-lying *D. polytomum* grounds in Central Bohemia, such as Dobřiš and the Sazava region. For example, in 1935, Dobřiš (400 m.), 2 per cent.; Pleše (500 m.), 4 per cent.; Kunžak (600–700 m.), 8 per cent.; Silesia (600 m.), 12 per cent.; Riesengebirge Mountains (800 m.), 10 per cent. In 1936 much the same gradation was observed: Dobřiš, 4 per cent.; Sazava region (500 m.), 1 per cent. and absent; Pleše, 9 per cent.; Kunžak, 8 per cent.; Silesia, 24 per cent. The highest recorded was 26 per cent. at Kunžak, in the South Bohemian mountains, in 1933. This was the highest figure recorded for any larval parasite.

Lamachus is distinguished among the *D. polytomum* parasites by being a rather large, slender insect, with elongated abdomen, long, thin, curling antennae, very long legs and wings, the areolet of which is very small and triangular. The female is distinctly darker than the male, being of a general blackish colour above, relieved only by yellow tegulae and scutellum and pale yellow edges of the abdominal segments. The face and lower side of the abdomen is bright yellow in fresh specimens. The male has a conspicuous yellow patch mid-dorsally on the third and fourth abdominal segments, and the underside is entirely yellow, from bright to pale lemon. The legs of both sexes are yellow to reddish yellow, with the hind tarsi black and hind tibiae black distally, but with a broad white ring centrally, sometimes extending to the base. This species can be distinguished from *L. marginatus*, which it most closely resembles, by the following characters: In the male, the metapleurae are mostly yellow, instead of black; abdomen conspicuously yellow centrally; hind tibiae much more broadly white; puncturing of mesopleurae less deep and conspicuous, second abdominal segment more strongly coriaceous: in the female the abdominal segments are more strongly sculptured; hind tibiae more conspicuously marked with white; mesopleurae with punctures less distinct. Length, from 11·5 to 13·0 mm.

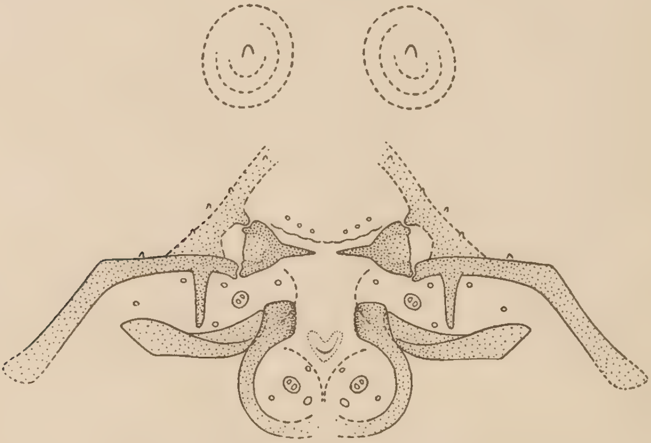


Fig. 13. Mouth-parts of mature larva of *Lamachus* sp. (× 80).

Lamachus is primary and endoparasitic on the larval stages of *D. polytomum*, laying its eggs in the fourth and fifth stage larvae. It is a large egg, from 0·98 to 1·08 mm. long, by 0·3 to 0·36 mm. wide, strongly curved and tapering equally at each end (fig. 1*e*). The chorion is of a dark brown colour and unsculptured. In both size and shape it is easily distinguished from the eggs of *Holocremnus*. The primary larva hatches from a hole at one end of the egg and is of caudiform type. It is slightly larger than that of *H. ratzeburgi*, and may be distinguished from it by the differently formed labial ring and the presence of papillae on the tail, as well as by the size (fig. 11*b*). In length it measures 1·5 mm. × 0·3 mm., the tail being 0·2 mm. long. The head-capsule averages 0·34 mm. long by 0·25 mm. wide. The skin of the thirteen segments is smooth, only the tail bearing papillae. The larva feeds internally until full-grown, when it leaves the perfectly empty host skin and spins a thin white cocoon within the host cocoon. As with *Holocremnus*, the egg-shells are always to be found in the empty host skin. Development rarely proceeds until the host has entered the prepupal stage and spun its cocoon. The period elapsing before the emergence of the adult varies considerably in the first generation, from 10 to 40 days, the average being three weeks. This is bivoltine, as is the host.

The mature larva (fig. 13) has characters quite distinct from those of the other Tryphonine parasites, *Exenterus* spp., but has characters in common with others of the MESOLEPTINAE, which have been examined. Most characteristic is the broken appearance of the labial ring, due to the chitin of the basal sector being much thinner and unpigmented. This is very obvious in the living larva. Other characters of this species are : The elbowed hypostoma ; the short maxillary struts ; the labial struts adjoining the top of the labial ring, above the level of the salivary opening, which itself is rather deeply placed within the labial ring, and distinctly U-shaped ; the labium is divided into two lobes, as in *Holocremnus*, but without the Y-shaped pigmented area between them ; the epistoma is incomplete ; the mandibles are similar to those of *Holocremnus*, with pointed, inwardly curved teeth unarmed with bristles. The skin structure (fig. 16*i*) is similar to that of *Holocremnus*, but the scales are more sharply conical and more closely packed. The spiracle (fig. 15*i*), as in the other endoparasitic larvae, is small and without closing apparatus. The flattened-spherical atrium, a little over 0·02 mm. in diameter, has very faint annular thickenings basally. The thin-walled stalk, slightly annulated apically, leads directly into the tracheal branch without any closing apparatus. The whole spiracle is 0·05 mm. long.

It is evident from the Bohemian records quoted above that this parasite is capable of attaining quite a high degree of control on *D. polytomum* under the right conditions, and its liberation in Canada has been advised from the first. Some 6,850 specimens have been liberated, but it has not yet been recovered from local sawfly hosts. Judging from the distribution in Europe, it is not so suited to a low, dryish climate, but attains its maximum effect in the warm but damp climate of moderately high mountains, between 600 to 800 m., such as the Silesian and South Bohemian ranges.

17. **Lamachus spectabilis,** Holmgr.

This is the only species of *Lamachus* previously recorded as parasitizing *D. polytomum*, in Finland by Forsius (1932). In the present work it has been found mainly as a parasite of *D. abieticolor* in various parts of Bohemia, also bred from *D. sertifer* in the Riesengebirge, and on a very few occasions it has been reared from larvae of *D. polytomum* in the Erzegebirge and the South Bohemian Mountains.

This is distinct from the previous and more abundant species, as an altogether darker insect. The yellow shoulder markings are missing, and on the metathorax the markings are darker and less distinct ; the pale edges of the abdominal segments in the female are much less conspicuous, often so dark as to be hardly differentiated ; in the male the yellow patch on the abdomen is small and duller ; the face is less conspicuously yellow ; in the hind legs, the femora and tibia are mainly black, the white ring on the latter being small and restricted to the basal segment. This is slightly smaller than the previous species, measuring from 10 to 12 mm. in length.

Judging by its prevalence on *D. abieticolor* this might prove a useful parasite of *D. polytomum*, but our knowledge is too scanty to advise upon this point.

18. **Exenterus tricolor,** Roman.

Members of the genus *Exenterus* are parasitic exclusively upon larvae of the DIPRIONIDAE, but this species is one of the least known, having only one previous host record, from *D. polytomum* in Finland (Forsius, 1932). During the present work this species has been bred from *D. polytomum* mainly in the Erzegebirge and Riesengebirge Mountains, on both the Saxon and Bohemian sides, and once from South Bohemia. It has also been obtained in a few instances from *D. sertifer* in the Riesengebirge, and two specimens from this host in Sweden. Thus its distribution corresponds always with the more mountainous, colder, and wetter regions in which the host is found, in contrast to the next species, *E. adspersus*, which occurs all over the lower regions of Bohemia. It is capable of attaining quite an abundance. At Tyssa in 1932, 19 per cent. of *D. polytomum* larvae of the first generation were destroyed by this parasite, and 17 per cent. of the second generation. In Saxony in the same year it accounted for 11 per cent. and 8·5 per cent. of the first and second generations respectively. Since then its numbers at Tyssa have declined somewhat, there being at the same time an increase in another larval parasite, *Holocremnus ratzeburgi.* In 1933 only 10 per cent. of larvae were destroyed, in 1934 this had fallen to 3 per cent. In the Riesengebirge, where only a single generation of the host occurs in a year, the percentage parasitism by this species was always low, from 2 to 4 per cent. *E. tricolor* was also bred in small numbers from *D. sertifer* in the Riesengebirge in 1933 and 1934.

The species of this genus are extremely difficult to separate owing to the range of individual variation. Morley (1911) describes fifteen species as British, but on the Continent Schmiedeknecht (1911) states that of the seven species described only two can be distinguished with certainty, the remainder being colour variants of these. Thomson (1883 and 1889), however, gives fairly clear descriptions, making the separation of 6 species possible. The identification of our species has been based on these descriptions. Among the parasites of *D. polytomum*, *Exenterus* can be distinguished by the absence of tibial spines on the hind legs. Beyond this it can be recognized at once as a handsome black insect with conspicuous yellow markings on the body and legs. The hind margins of the abdominal tergites are typically banded with yellow. The three species of *Exenterus* occurring on *D. polytomum* are by no means easy to separate from one another and from other members of the genus. *E. tricolor* is fairly easily recognized by the apical segments of the abdomen being ventrally and sometimes laterally of a reddish colour. In the female the last abdominal sternite is long and acute instead of broad and obtuse as in the other species. The face, legs, and underside of the thorax are more widely marked with yellow than in the other species, the front and middle legs being entirely yellow with the exception of the femora, which are marked with black, sometimes only a black spot. *E. marginatorius* can be distinguished from both these species, and from the other species in the genus except *E. abruptorius*, by the well-marked ridge or keel along the anterior margin of the mesosternum. From *E. abruptorius*, which it most closely resembles, it can be separated by the claws in the female being not pectinate. *E. adspersus* can be distinguished from *E. marginatorius*, apart from the above character, by the finer punctation of the thorax, and by the greater amount of yellow on the front legs, the coxae and femora only being marked with black, while in *E. marginatorius* the femora and tibiae are strongly black above and yellow below. Further than this, *E. marginatorius* is markedly larger and stouter, with the markings more strongly developed, especially the yellow banding of the abdominal tergites being much broader on the first two segments. *E. tricolor* and *E. adspersus* are smaller and more slender, with the yellow markings, especially on the abdominal tergites, less pronounced. *E. tricolor* averages 6·8 mm. in length.

Regarding the biology of *E. tricolor*, adults have been captured early in June, flying round the sunny margins of spruce plantations, and again in September and even mid-October. These late records are of adults captured round wire cages where numbers of second generation larvae were being reared to maturity. It has been found to correspond with the host in its life-history, having two generations in most of Bohemia and a single generation in the Riesengebirge. The eggs are laid externally on the larva of *D. polytomum*, most commonly on the dorsal or lateral aspect of the thoracic segments, though occasionally far back on the body or attached to a leg. Larvae thus affected show no traces of having been stung by the parasite. Oviposition is on the fourth or fifth stage larvae or prepupae, the mature larvae being most often attacked. Hatching does not occur until after the spinning of the host cocoon, and the parasite larva feeds externally on the prepupa within the cocoon. It will be seen, then, that the host goes through one or two ecdyses between the oviposition and hatching of the parasite, and this necessitates a special modification of the egg in order that it shall not be lost during these moults.

The egg (fig. 1*c*) is yellowish-white in colour and covered with a scale-like sculpturing, of an elongated pear-shape, the narrow end tapering acutely with the chorion prolonged into a short stalk. This stalk is embedded in a dark-coloured, hard, button-shaped disc, of quite a different substance from the chorion. The egg averages 0·5 mm. long by 0·18 mm. at the widest point ; the stalk is 0·05 mm. long and the dark disc 0·06 mm. in diameter. The stalk penetrates the skin of the sawfly larva and the disc lies under the skin embedded in the muscle layer, with its diameter at right angles to the stalk. Thus the disc acts as an anchor, and so firm is this attachment that, under natural conditions, 80 to 90 per cent. of the eggs survive the one or two subsequent moults of the host larva. This is possible because of the elasticity of the freshly shed skin, the *Exenterus* egg either pulling through the tiny hole in the skin at the point of attachment, or a small piece of skin breaking away and remaining round the base of the stalk, leaving a jagged hole in the old skin, through which the egg easily slips. If the moult is prolonged or difficult, or in a dry atmosphere, the egg is much more likely to be torn from its anchorage and lost with the cast skin. In just under 50 per cent. of a number of cases kept under observation in a laboratory the eggs were lost on ecdysis in this way, but such heavy losses were probably due to the dry atmosphere in the rearing glasses. The dependence on humidity for the survival of the eggs must have an important bearing on the distribution and success of this parasite in the field, and this will be discussed later. Even after the egg has come through the ecdysis, it is subject to much mechanical action during spinning, when there is great danger of its being knocked off by the coarse resinous threads of the cocoon inside which the prepupae is actively turning. Hatching occurs in from 5 to 15 days in the first generation, but in 10 days to a month in the autumn. It is of the greatest importance to the parasite that hatching should not take place until the cocoon is formed, otherwise the young larva is invariably lost in the ecdysis or spinning and is unable to regain the newly moulted host.

The newly hatched larva (fig. 2*b*) is of a dull white colour, bluntly fusiform in shape, 0·55 mm. long and 0·23 mm. wide. The head is well chitinized and bears a pair of strong, curved mandibles and a pair of small antennae. The body, of 13 segments, has a lateral armature of long, strong hairs, almost 0·1 mm. in length, giving the primary larva a very characteristic hairy appearance, easily visible without a lens, by which it can be readily distinguished from those of all the other parasites. The base of the hairs, especially the larger ones, is apparently muscular, as they have a limited power of movement. The arrangement of the hairs can be seen from the illustration. The last segment has a pair of caudal bristles or setae, which probably function in retaining a hold on the egg-shell when the larva is hatching. Under high magnification, the cuticle can be seen to be covered with small slender setae, similar to those of the full-grown larva (*q.v.*). By means of these setae and hairs, the primary larva can move about in a very active manner when necessary. The larva hatches from the outer pole of the egg and immediately fixes itself by flexing the body until the head reaches the skin of the host and a grip can be obtained with the mandibles. For an hour or two it remains in this position with the tail still retaining a hold in the egg-shell, doubtless by means of the caudal bristles. After it has fed for this short while, the hold by the tail is released, and during the rest of the first stadium it remains fixed to the host by the mandibles alone, never relaxing its hold or altering its position unless accidentally knocked off. In this eventuality it can move about actively, and soon regains its hold upon the host. During this time the host is still living, but soon after the first moult of the parasite larva it is found to be dead. The exact point at which death occurs and the reason are not clear. On the first ecdysis the parasite loses its long motile hairs, but still has a skin armature of minute fine setae. It now becomes more active and does not remain fixed to the host but moves about, feeding at different positions. Should more than one *Exenterus* egg be laid the young larvae will feed together during the first stadium, but during the second stadium one invariably predominates and kills and devours the others. In the first or summer generation there is now an intensive feeding period, the larva passing through five stadia, to become full-grown in a little over a week from the time of hatching. The mature larva now spins a semi-transparent, whitish, papery cocoon, excluding the completely empty and shrivelled host remains, and enters the prepupal stage. This lasts five days to a week in the first generation, 3 to 6 days as an eonymph, and one to three days as a pronymph. In the second generation the larva usually completes its feeding before the onset of cold weather and passes the winter in the eonymphal stage, appearing only in the following spring. Occasionally larvae of the second generation go into hibernation in the second or third instars and complete their development in the following year. As might be expected, this is of more frequent occurrence in the colder regions. Pupation occurs shortly after the assumption of the pronymphal stage in both generations, being preceded by defaecation and ecdysis. The pupa libera is at first clear white in colour, only the eyes being dark red. It darkens rapidly and in 4 to 5 days the adult emerges.

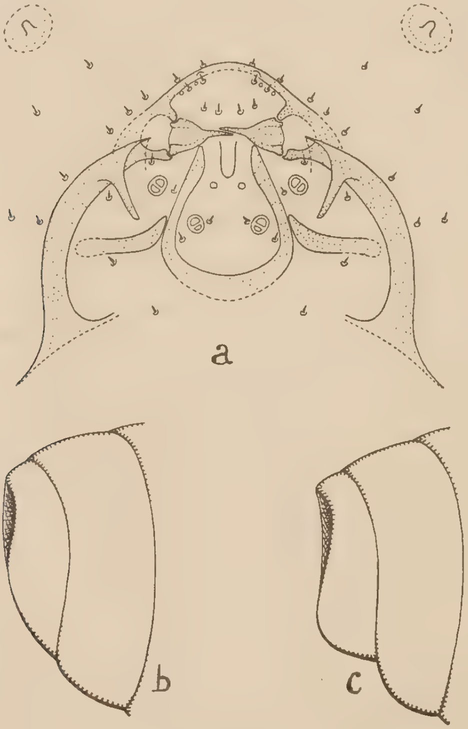


Fig. 14. *a*, mouth-parts of mature larva of *Exenterus tricolor* (× 80) ; *b*, last abdominal segment of *Exenterus adspersus* ; *c*, last abdominal segment of *Exenterus* sp.

The mature larva of *E. tricolor* (fig. 4*c*), shining creamy-white in colour, 6 mm. long by 2·7 mm. broad, does not differ, on casual inspection, from the other parasites, except that it is considerably smaller than *Microcryptus*, *Holocremnus*, *Lamachus*, and *Pimpla*. Under the microscope the distinctive features of the head and skin are easily distinguished. The chitinous head appendages (fig. 14*a*) are not only smaller but also more compact than those of the four above-mentioned genera. It lacks the clypeal arch, chitinized salivary opening and ligula of the Cryptines. The complete, horseshoe-shaped labial ring of approximately equal width throughout distinguishes it from *Holocremnus*, *Lamachus*, and the Pimplines. Further distinctive characters are the rather slender mandibles with long sharp points without any bristles, the complete epistoma, the well-developed, curved hypostoma, not widely separated basally ; the labial struts adjoining the labial ring nearly mid-way between base and apex. The skin armature of *Exenterus* (fig. 16*g*) is very characteristic, consisting of a number of fine, slender setae, 0·024 mm. in length, with rather swollen, rounded bases set in slightly sunken pits in the cuticle. They are closely arranged all over the body segments, and even in the living larva, under comparatively low magnification, they impart a distinctive, slightly downy appearance to its skin.

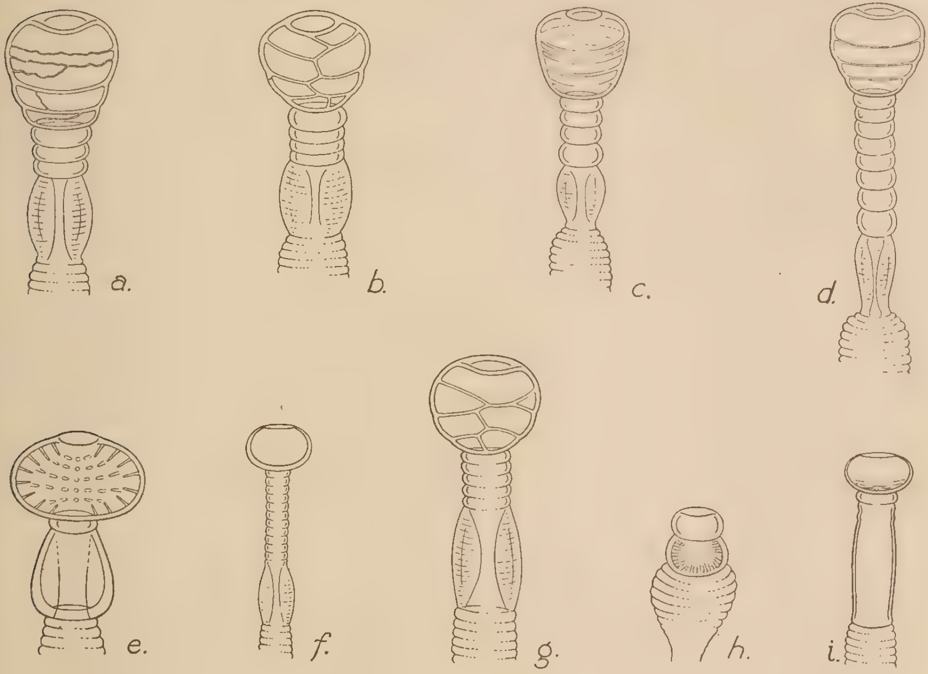


Fig. 15. Spiracles of (*a*) *Microcryptus basizonius* ; (*b*) *Spilocryptus abbreviator* ; (*c*) *Habrocryptus polytomi* ; (*d*) *Hemiteles areator* ; (*e*) *Pimpla alternans* ; (*f*) *Delomerista* sp. ; (*g*) *Exenterus tricolor* ; (*h*) *Holocremnus ratzeburgi* ; (*i*) *Lamachus* sp. (all × 450).

The spiracle (fig. 15*g*) also affords a useful distinctive character. The atrium, almost spherical, 0·035 mm. in diameter, flattened on top, has a fine, reticulate thickening to the inner surface. A short annularly thickened stalk leads into the thick-walled closing apparatus. The whole spiracle is 0·08 mm. long. No attempt has yet been made to distinguish between the larval stages of the four species of *Exenterus* found on *D. polytomum* (mainly through lack of time), but small differences do exist and it is hoped they may be described later. The above description of *E. tricolor*, however, is distinctive of the larvae of these four species and serves to separate them from those of other genera.

Exenterus tricolor, and the other species also, have one extrinsic disadvantage, which seriously impairs their efficiency. It has been pointed out that the survival of the eggs is dependent on a high atmospheric humidity, enabling them to come through the last one or two moults of the host, and that larvae hatching too soon invariably perish. In the laboratory, 50 per cent. losses were incurred in this way because of the low humidity, but the loss in the field is probably much lower, less than 20 per cent. This will inevitably lessen the parasite's efficiency and chances of its becoming a very important controlling agent. Another effect is on the distribution of the parasite. It would be expected to attain its maximum efficiency in regions of high humidity or heavy rainfall. Actually this species has only been found in the wet mountainous regions of Bohemia and Northern Europe. Here it is capable of attaining a fairly high parasitism, but it is significant that this was highest (at Tyssa) in 1932, a year of heavy rainfall, and the rate fell off very sharply in the following years, when the rainfall was considerably below normal. Its only appearance in

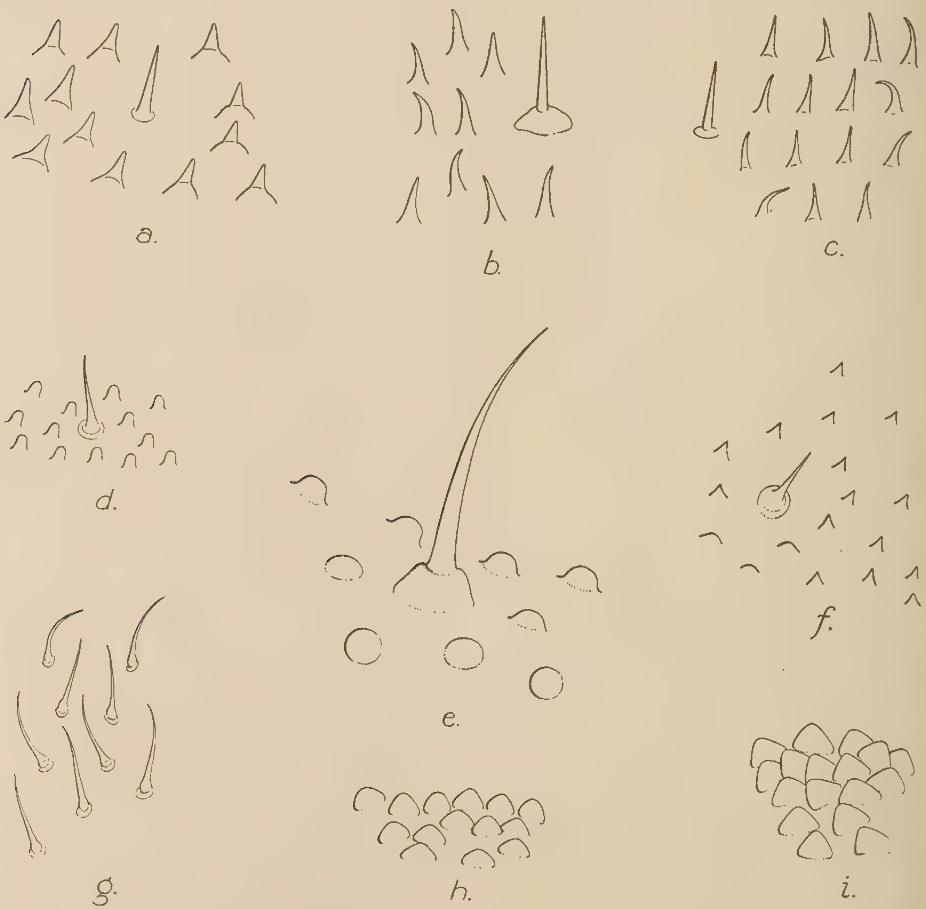


Fig. 16. Skin armature of (*a*) *Microcryptus basizonius*; (*b*) *Spilocryptus abbreviator*; (*c*) *Habrocryptus polytomi*; (*d*) *Hemiteles areator*; (*e*) *Delomerista* sp.; (*f*) *Pimpla alternans*; (*g*) *Exenterus tricolor*; (*h*) *Holocremnus ratzeburgi*; (*i*) *Lamachus* sp. (all × 450).

South Bohemia was in 1936, a year of exceptionally heavy rainfall (see Table, page 376). It is interesting to compare *E. tricolor* with *E. adspersus*, which latter has the same oviposition habits and therefore disadvantages, but is distributed over the lower (and drier) regions of Central and Southern Bohemia and Silesia. When the figures are comparable, *i.e.*, in the same season and from localities with a fair abundance of *D. polytomum*, *E. adspersus* has never shown so high a parasitism as *E. tricolor*. For example, in 1932: *E. tricolor*—Tyssa, 19 and 17 per cent., Tharandt, 11 and 8·5 per cent.; *E. adspersus*—Brdy Wald, 5·5 per cent., South Bohemia, 2 and 3 per cent. This latter species remained at about the same level, 3 to 5 per cent., in subsequent years, and only in 1936 (the very wet year) did it attain anything like the abundance shown by *E. tricolor*. Comparison in this year was impossible, as sufficient numbers of *D. polytomum* were not obtainable from the localities where *E. tricolor* was present. Evidently low humidity of the habitat acts as a severe check on both these species, more especially in the case of *E. adspersus*. In this case there is every chance of these parasites attaining their maximum efficiency in the wet mountain regions of the Gaspé Peninsula, or the coastal districts of New Brunswick. Such a marked climate preference should certainly be studied in making liberations.

E. tricolor was liberated in Canada in the first year of the work, but has not yet been recovered. This should by no means be taken as evidence of its unsuitability, since it has not yet been sent over in very great numbers, and the chances of its having already attained appreciable abundance at the points of liberation are consequently small.

19. **Exenterus adspersus,** Htg.

This is a fairly common parasite of the pine sawflies, having been bred from *D. pini* in France (de Gaulle, 1908), Russia (Meier, 1927 and 1929), and Finland (Hertz, 1933) and from *D. sertifer* in Bavaria (Jemiller, 1894) and Russia (Meier, 1927). It has also been bred on one occasion from *D. polytomum* in Finland (Forsius, 1932). During the present work it has been the commonest species of *Exenterus* parasitizing *D. polytomum*, being of more frequent occurrence than *E. tricolor*, because of its wider distribution, though the latter seems to attain greater local abundance, as has been pointed out above. It is of very widespread and regular occurrence throughout Czechoslovakia, being found in practically every sample of *D. polytomum* from every locality except the Riesengebirge. It occurs most frequently at the lower and middle altitudes where the host is found, and is rarest in the north of Bohemia, the Erzegebirge, where *E. tricolor* is most abundant. It is usually present in from 3 to 5 per cent. of the host larvae, but under favourable conditions has been found infesting as much as 13 per cent. Its incidence seems to depend largely on the prevailing climatic conditions, as will be discussed later. A single specimen of *E. adspersus* was bred from *D. sertifer* in the Riesengebirge in 1933.

The distinctive characters of the adults are set out in the section on *E. tricolor*. It is a rather larger species than the above, averaging 7·5 mm. in length, and has a stronger, less slender appearance, somewhat darker, with the yellow markings on legs and abdomen less conspicuous. The biology is in every way similar to that of *E. tricolor*, no differences having yet been observed, and the larval stages of the two species have not yet been distinguished. Consequently, it suffers from the same intrinsic disadvantage in that the eggs have to come through one or two ecdyses of the host in order that the parasite may survive. As has been pointed out in the case of *E. tricolor*, a fairly high atmospheric humidity is absolutely essential in order that a large proportion of the eggs may survive; consequently, it is to be expected that the distribution of such an insect and its seasonal abundance will be influenced mainly by humidity or rainfall. In the case of *E. adspersus* the distribution, for reasons not yet understood, is generally over the lower and middle heights of Czechoslovakia, not in the highest and wettest regions, as might be expected. Consequently, the influence of seasonal rainfall is, if anything, accentuated. This is very well demonstrated by the following sets of figures, showing the percentage of *E. adspersus* on *D. polytomum* in different localities and different years, the rainfall in mm. (the figure in brackets) being given for the six months May to September of each year. This is the important period of the year when *Exenterus* is active and subject to the influence of climate.

Table showing Incidence of E. adsperus *on* D. polytomum, *and Rainfall, in mm., for May to September.*

Locality	Brdy Wald	Hradec in Silesia	South Bohemia
Height in metres ...	400	600	550–700
1932	(423 mm.) 5·5%	—	(372 mm.) 8·1%
1933	(244 mm.) 5·0%	—	(347 mm.) 8·0%
1934	(254 mm.) 2·1%	—	(338 mm.) 4·2%
1935	(267 mm.) 2·5%	(449 mm.) 4·7%	(305 mm.) 4·0%
1936	(410 mm.) 6·0%	(547 mm.) 13·0%	(374 mm.) 10·0%

Not only does the abundance in each locality vary regularly with the summer rainfall, but it is also significant that on comparing the three localities, the higher the rainfall the greater is the incidence of *Exenterus*. It must be borne in mind that the picture is by no means a simple relationship of *E. adsperus* with climate ; many complicating factors are involved, the most important being the fact that the host is also favoured by a high humidity, and as there is always a lag between the increase of host and parasite, the true effect of rainfall on the parasite will always be damped down somewhat. There can be no doubt, then, that an abundant rainfall is definitely advantageous to the increase of this parasite. As has been pointed out in dealing with the previous species, this makes *E. adspersus* particularly suitable for liberation in parts of the Canadian infestation with an especially moist climate. Numbers of this species, totalling approximately four thousand, have been liberated every year since 1933, and the first recoveries were made in 1934. This and subsequent recoveries leaves no doubt as to the ability of *E. adspersus* to adapt itself to Canadian conditions, and it should prove to be a valuable component of the parasite complex that we hope will eventually be established.

20. **Exenterus marginatorius,** F.

This common larval parasite of the pine sawflies has only occurred in one isolated instance on *D. polytomum* in South Bohemia, though small numbers have been bred from *D. sertifer* in Czechoslovakia and in Sweden, and also from *D. virens* and *D. pallidum* in Czechoslovakia.

The adults of *E. marginatorius* are larger, stronger, and more striking looking than those of *E. tricolor* or *E. adspersus*. In size it averages 8·8 mm. long. The distinctions from the other species are detailed in the section on *E. tricolor*.

Scheidter (1934) gives a good description of the oviposition of this species on *D. pini*. As with the other members of the genus, oviposition is on the larvae or prepupae and development takes place within the host cocoon. We have not had sufficient numbers of this species to enable us to make a description or distinction of the larval characters.

There is no reason why *E. marginatorius* should not be introduced into Canada, if it could be obtained in sufficient quantity in Europe. The larger size of the Canadian race of *D. polytomum* and the different conditions might enable it to multiply with success upon this host.

21. Exenterus sp.

Recently a fourth species of *Exenterus* has been bred from *D. polytomum* closely resembling *E. adspersus*, but with certain features which definitely separate it from the others as a distinct species. It has not yet been possible to name this, but it is perhaps a new species. It has only been recognized in the most recent year, 1936. It is quite probable that it has always been present and has been confused with *E. adspersus*, especially considering the fairly wide distribution and good numbers recovered, but in this year the host, *D. polytomum*, was collected and studied in far greater numbers than had ever been done before, and this would tend to show up the less common parasites. It occurred in greatest numbers at the lowest altitudes and became progressively rarer in the higher regions. As *D. polytomum* is present in numbers in these low regions only in exceptionally wet years, such as 1936, this again might explain the previous absence of this species. The localities where it was recovered were: Sazava region (360 m.) 14 per cent.; Dobřiš in the Brdy Wald (400 m.) 3 per cent.; Pleše, South Bohemia (500 m.) 5 per cent.; Neu Bistritz, South Bohemia (550 m.) 5 per cent.; Hradec, Silesia (600 m.) 1 per cent.

The adults of this species of *Exenterus* resemble *E. adspersus* very closely in every respect—size, colour, markings, etc.—and are only to be recognized on the following characters, of which the shape of the last segment in the female is the most distinctive:—

Exenterus adspersus	*Exenterus* sp.
Last abdominal segment of female broadly convex (fig. 14*b*).	Last abdominal segment of female right-angled (fig. 14*c*).
Front and middle coxae black, yellow beneath, tarsi yellow, hind coxae black.	Mid coxae almost or entirely yellow, hind coxae yellow, black above.
Propodeon less conspicuously yellow marked.	Propodeon more conspicuously yellow marked.

Nothing is yet known of the biology of this species, except that it is a primary larval parasite of *D. polytomum* developing within the cocoon, but its close resemblance to *E. adspersus* would lead one to expect their life-histories to be similar. In distribution it seems to occupy an even lower region than *E. adspersus*, just as *E. adspersus* is distributed at a lower altitude than *E. tricolor*, there being, of course, considerable overlapping. Further details of its biology and relationships with the other members of the genus will be of very great interest, and it is hoped that it will soon be possible to supply them. Meanwhile, there need be no fear as to the advisability of liberating this undoubtedly primary parasite into Canada; indeed, it has probably already been liberated in some numbers.

22. Microbracon sp.

Only one specimen of this unidentified species of *Microbracon* was bred from a second generation cocoon collected at Zbiroh, Central Bohemia, in 1932.

23. Monodontomerus dentipes, Dlm.

This Chalcid has been recorded from a number of Hymenopterous and Lepidopterous hosts, frequently as a secondary on various Ichneumonids and Braconids. It can, however, act as a primary parasite on pine sawflies, having been bred from *D. pini*, L., in Holland (Ritzema Bos, 1919) and Germany (Scheidter, 1934) and from *D. pini* and *D. similis* in Poland by Sitowski (1929), and from *Diprion* spp. in Poland by Mokrzecki (1933). Sitowski observes that it may often be hyperparasitic. It already occurs in North America, where it was observed by Weiss (1917) to be heavily parasitizing *D. similis* in New Jersey in 1916, and subsequently proved to be one of the most effective checks upon this species in New Jersey and Pennsylvania (Hartley, 1923).

This is probably one of the most important parasites of *D. polytomum* in Europe, and it has been found with regularity in cocoons from every locality in Czechoslovakia, frequently in quite high proportions. It is difficult to estimate the percentage reached by such cocoon parasites, firstly because a large number of cocoons have not always been obtainable from each locality ; secondly, because the generations of these small Chalcids by no means synchronize with those of the host ; they are constantly emerging and ovipositing in new cocoons, so that the amount of destruction is cumulative from the time the first *Diprion* cocoons appear. The proportion of cocoons parasitized will depend entirely on when they were collected. Collections made soon after spinning have shown an entirely different parasitism from those made shortly before emergence. Even a big sample taken throughout the time cocoons are available will necessarily underestimate the effect of such parasites. When sufficient numbers of such cocoons have been collected, *M. dentipes* has always been present, the percentage varying from 4 or 5 to 40 per cent. The abundance varies tremendously from year to year, and there is no indication of preference for certain terrains as in many of the other parasites. Frequently, when *Eutelus subfumatus* is abundant, *M. dentipes* will be comparatively rare, and *vice versa*. The importance it can attain is shown by a few figures : Brdy Wald area, 1932, 22 per cent., 1933, 35 per cent., 1934, 16 per cent., 1935, 9 per cent., 1936, 6 per cent. ; South Bohemia area, 1933, 28 per cent., 1934, 18 per cent., 1936, 10 per cent. During these investigations *M. dentipes* has been bred from *D. pallidum* in Bohemia, but never from *D. pini* or *D. sertifer*.

This species is characteristic among the Chalcid parasites of *D. polytomum*, as the only one with a long, exserted ovipositor. It is a large, dark species, the head, thorax, and abdomen having a dark, metallic greenish-blue sheen. The hind coxae are very large, three times as large as the others, with a strong, blunt tooth on the posterior edge distally, and the femora are also broad and strong, and with a well developed tooth distally. The wings are faintly clouded with brown and the stigmal area has a distinct dark brown patch. The stigmal vein is very short, much shorter than the postmarginal. The ovipositor is exserted and almost as long as the abdomen. Length 2·75 to 3·5 mm. Ovipositor 1·0 mm.

This has always been found as a primary parasite on *D. polytomum*, although, in view of the records, it is quite possible that it may occasionally act as a secondary. It is a parasite of the prepupal stage, a female laying always more than one egg, usually 5 or 6, in the sawfly cocoon. Fifteen eggs have been found in a single cocoon. The egg (fig. 17*a*) is very large for such a small insect, being 0·7 mm. long by 0·2 mm. broad, glossy white in colour and covered with symmetrical rows of minute spicules. In shape it tapers abruptly at the broader end, rather gradually at the other end towards the micropyle, a slight knob. The life-history of *M. dentipes* has not been fully worked out ; all attempts to breed it in captivity have failed, probably because there is a fairly long period, a month or two, between the emergence of the adults and their sexual maturity. In repeated experiments these parasites have neither copulated nor shown any inclination for oviposition in the three or four weeks they have survived in captivity, whereas the other common Chalcids, *Microplectron*, *Dibrachys*, and *Eutelus*, have all copulated and oviposited soon after emergence.

The larvae of *M. dentipes* feed externally on the prepupae, which they consume completely. The average number of adults emerging from a cocoon is 4·5, but as many as 12 have been reared from a single host. It has a fairly slow development for a Chalcid. Larvae have been found to take 3 to 4 weeks to reach maturity, and the pupal period has been found to last 3 weeks in early spring, though it may be shorter in summer. Hibernation takes place in the prepupal stage inside the host cocoon, pupation occurring in April and the first adults emerging in May. Adults have been found on the wing throughout every month in summer and into late September. This may be due to a long length of life, but is also due to the fact that all the members of one brood do not by any means emerge at one time ; a full month has been found to elapse between the emergence of the first and last insects from one cocoon, and it very frequently happens that some larvae of late broods pupate and adults emerge in autumn, while others in the same cocoon go into hibernation and the adults appear in the following spring. Because of the slow development and the

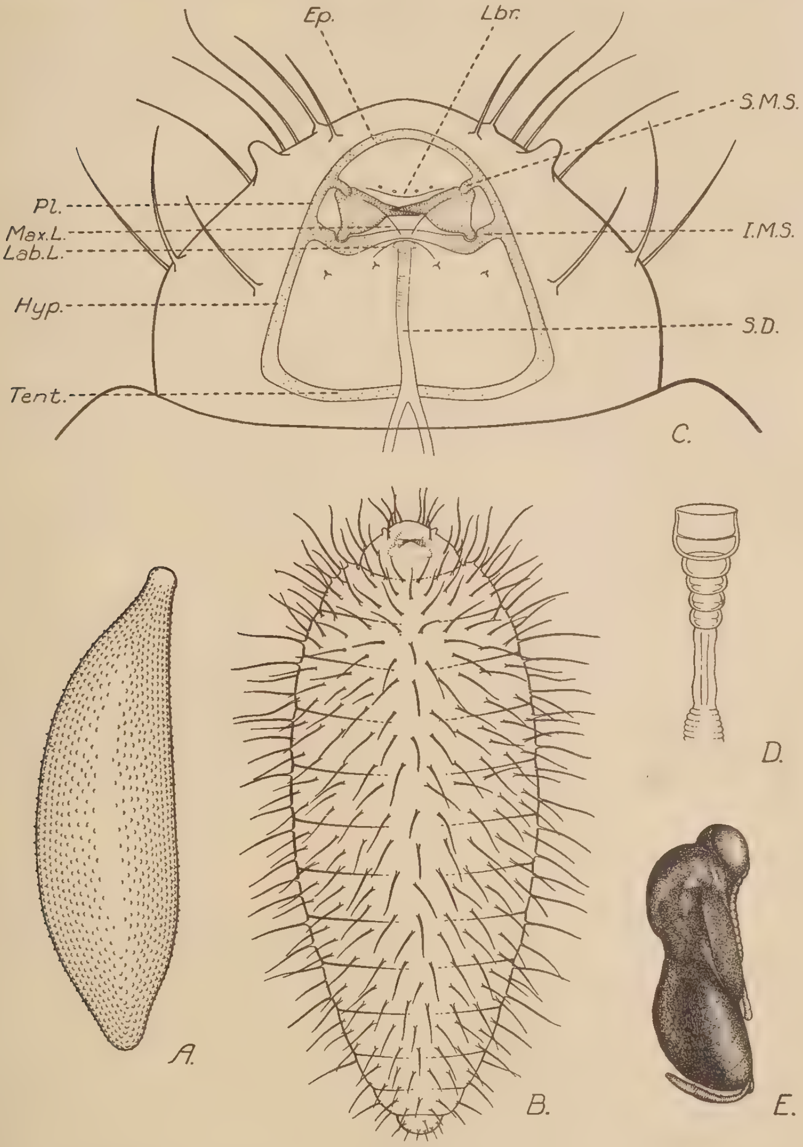


Fig. 17. *Monodontomerus dentipes* : (*a*) egg (× 90) ; (*b*) mature larva (× 25) ; (*c*) head of mature larva (× 150) ; (*d*) spiracle (× 450) ; (*e*) pupa (× 12·5) ; *Ep*, epistoma ; *Hyp*, hypostoma ; *I.M.S*, inferior mandibular strut; *Lab*, labium ; *Lbr*, labrum ; *Max.L*, maxillary lobe ; *Pl*, pleurostoma ; *S.D*, salivary duct ; *S.M.S*, superior mandibular strut ; *Tent*, tentorium.

time taken in reaching maturity there are probably only two generations in the year, with a great deal of overlapping, but with favourable weather, such as a warm and early spring and late autumn, there is the possibility of a third generation.

The larvae of this species can be distinguished from those of all the other parasites by their very hairy appearance, easily visible to the naked eye, and apparent even in the first stadium. The full grown larva (fig. 17*b*), consisting of a head and 13 body segments, is semi-translucent, creamy white in colour and thickly covered with long white hairs, 0·3 mm. in length. It measures 3·5 mm. long by 2·0 mm. broad. The head (fig. 17*c*), 0·5 mm. in width, is also furnished with long hairs arranged in a definite pattern. There are also a pair of short, papilla-like antennae, and a labrum behind which opens the salivary duct. There are two pairs of setose papillae on the labial region. The internal head skeleton has the same fundamental basis as in the Ichneumonid larva, but is simpler. The well developed, sharply pointed mandibles articulate on the superior and inferior mandibular struts. The superior strut bears the condyle which fits into a fossa on the top of the mandible's triangular base, the lowest angle of which bears a condyle fitting into a fossa on the inferior mandibular strut. The superior and inferior struts are joined by the pleurostoma and the inferior struts are continuous below the pharyngeal opening. The pleurostoma is continued forward to form an arch, the epistoma, and backwards to form the hypostoma, whose lower end is joined by the inwardly projecting arch of the tentorium, passing behind the pharynx and salivary duct. The two branches of the latter fuse together at about this point. This type of head structure is constant, with small modifications, throughout the Chalcids. Nine pairs of spiracles are present, in the second to tenth segments. The atrium is 0·02 mm. wide and the whole spiracle 0·04 mm. long, the construction is shown in fig. 17*d*.

The pupa (fig. 17*e*) at first pale yellow, but gradually turning to a glossy black, is easily recognised by the long recurved ovipositor, closely adhering to the dorsal surface of the abdomen.

There was no hesitation in introducing into the infested areas such an important parasite of *D. polytomum* with a proved ability to acclimatise itself in North America. In the first year of parasite liberations, 1933, 13,731 individuals of this species were liberated in Canada, a part of these coming from Europe but the majority having been bred from *D. similis* cocoons collected in Ontario. Increasing numbers of these insects have been sent from Europe in subsequent years, and it has been recovered from cocoons in the infested areas, so that there is good reason to hope that it may eventually develop into an important enemy of *D. polytomum* in Canada.

24. Habrocytus sp.

Most of the species of this genus are hyperparasitic upon a large variety of hosts, and there seem to be no records from TENTHREDINIDAE. During the present work it has been obtained on only three or four occasions from cocoons of *D. polytomum*, collected in South Bohemia and the Böhmerwald in 1934. It has also been bred from cocoons of *D. pallidum* from the same locality. In all cases it was hyperparasitic.

The present knowledge of this group does not permit of the identification of this species. It is easily recognized among the other Chalcid parasites as a large species, 3·5 mm. long, with a dark metallic green lustre tinged with bronze. The abdomen is sharply pointed and keeled, with the ovipositor not exserted. Occiput not carinated. Clypeus with four well-developed teeth. Antennae inserted in the middle of the face, ten-jointed. Tarsi five-jointed, hind tibia with only one spur. Wings clear, with marginal vein shorter than subcostal and postmarginal longer than stigmal.

It is obvious that such a hyperparasite would be very undesirable in Canada.

25. **Eutelus subfumatus**, Ratz.

This Chalcid has been previously recorded from *D. pini* (Cameron, 1889) and *D. sertifer* (de Gaulle, 1919) in France. It ranks with *Monodontomerus dentipes* as one of the most important parasites of *D. polytomum* in Europe. It has occurred with regularity in every locality in Czechoslovakia, very frequently in abundance. The difficulty of estimating the true rôle played by such a cocoon parasite has already been pointed out, but, considering the high parasitism occasionally recorded, the accumulated effect of *E. subfumatus* must prove a very important check on the increase of *D. polytomum*. In 1936 fairly large collections of cocoons were made from most of the collecting localities in Bohemia, and from the figures obtained,

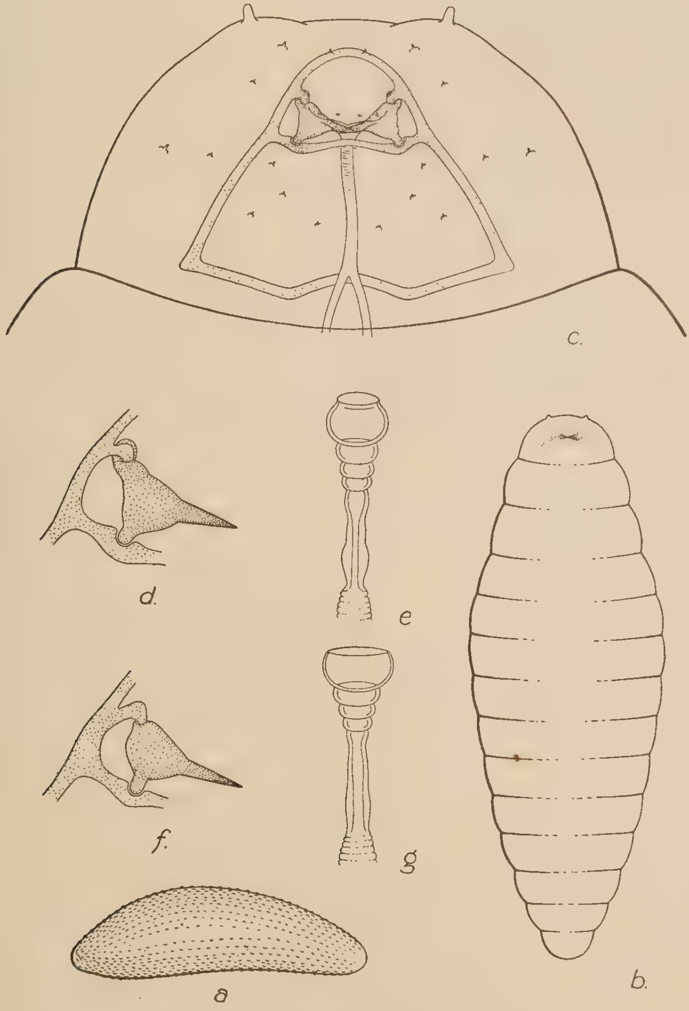


Fig. 18. *Eutelus subfumatus*: (*a*) egg (× 90); (*b*) mature larva (× 25); (*c*) head of mature larva (× 150); (*d*) mandible (× 450); (*e*) spiracle (× 450); (*f*) mandible of *Dibrachys cavus* (× 450); (*g*) spiracle of *D. cavus* (× 450).

which are quite representative, an idea of the importance of this parasite can be gathered:—Dobřiš, 5 per cent., Sazava region, two localities, 9 and 13 per cent., Kunžak and Pleše, South Bohemia, 12 and 20 per cent. respectively; Silesia, 23 per cent. It always appeared in special abundance in the Erzegebirge and the South Bohemian Mountains. Here a 30 per cent. parasitism has been recorded several times, and occasionally, from small samples of cocoons collected late in the season, as many as 60 per cent. have produced *Eutelus*. This parasite has also been bred from *D. pini* and *D. pallidum* in Bohemia.

Eutelus subfumatus may be distinguished among the Chalcid parasites of *D. polytomum* by the brilliant metallic green colour of the head, thorax and abdomen, and the bright yellow legs and antennae, the latter tipped with brown. The occiput is not carinated and the clypeus does not bear a median tooth. The antennae are inserted at the base of the face, below a line drawn from the base of the eyes. Wings clear, with the marginal vein shorter than subcostal, and stigmal shorter than postmarginal. Length between 1·0 and 2·5 mm., depending mainly on the number emerging from a cocoon.

E. subfumatus is a primary parasite of *D. polytomum*, ovipositing within the cocoons on the prepupa or pupa. The egg (fig. 18*a*), 0·45 mm. long by 0·13 mm. wide, is somewhat curved, tapering sharply at the broad end and gradually at the other. In shape it resembles a gherkin. It is white, and the surface studded with minute, round tubercles. A number of eggs are laid by each female in a cocoon, from 3 or 4 up to 30, the average being 10. On hatching, the larvae feed on the host prepupa or pupa, killing it after a day or two, and finally devouring it completely if enough larvae are present. There are five active stadia, the last, or mature larval, gradually merging into the prepupal on the cessation of feeding. After two or three days as a prepupa, in summer, pupation takes place, and in a further two or three days the adults emerge, biting a very small hole in the side of the cocoon. In autumn the prepupae go into hibernation, pupation taking place next spring. The number of adults emerging from a cocoon averages 9·5, but frequently from 20 to 25 survive and emerge. The length of the life-cycle depends mainly upon temperature in the localities investigated. At midsummer in the lower regions of Bohemia, with a monthly mean temperature of 18 to 20°C., it was three weeks. Later in the year, or in the high mountains, with a monthly mean of 11 to 15°C., it was five weeks. It was found to pass through three or four generations in the year at the lower and warmer altitudes in Central Europe. Adults have been found on the wing in the Erzegebirge Mountains in Saxony at the end of April. These would have an opportunity of laying in unemerged *Diprion* cocoons at once. The second generation emerges late in June, when some cocoons of the first generation of *D. polytomum* are already present. The third generation, because of the higher temperatures in July, emerges at the end of this month or in August, while there are still late cocoons of the first generation available. The fourth generation does not emerge until the middle of September, in time for the second generation host cocoons. The insect passes the winter in the mature larval or prepupal stage, going into hibernation in late September. Naturally the successive generations are by no means so clear cut as the above picture; there is considerable overlapping owing to late emergences, etc., and cold and wet weather may so prolong development and shorten the flight and oviposition periods as to cut out a generation altogether.

The mature larva (fig. 18*b*), of typical Chalcid form, is rather elongate, 3·0 mm. long by 1·0 mm. wide, tapering posteriorly from the widest part in segments 4 and 5, and somewhat narrowed anteriorly, the hemispherical head being 0·5 mm. wide at the base. It is yellowish white in colour, glistening and semi-transparent, with a perfectly smooth cuticle, only a few minute papillae being discernible under high magnification. The glossy-white head (fig. 18*c*) shows three lobes, two epicranial, bearing the antennae, and one labial, below the mouth. The labrum is obtusely pointed, and bears two pairs of sensillae, marginally. There is also a definite arrangement of spicules on raised, swollen bases, the distribution on the anterior aspect of the head being characteristic, and shown in the illustration. The head skeleton is of the usual Chalcid type, described above under *Monodontomerus dentipes*, only the general shape and lay out, and the relative proportion of the components to one another, afford distinctive characters useful for separating the different species. The larva of *Eutelus* can be distinguished at once from that of *Monodontomerus* by the absence of hairs, but it is not easy to separate from those of the other Chalcids, especially from the hyperparasite *Dibrachys cavus.* It can be distinguished from *Microplectron* by the different arrangement of spicules on the head ; also by the narrower, more rounded epistoma and the different shape of the mandibles (fig. 18*d*), and of the spiracles (fig. 18*e*). Practically the only distinctions from *D. cavus* lie in the shape of the mandibles and spiracles. Such minute differences can only be discerned in a good preparation under the microscope. They are difficult to describe and can be best appreciated from a study of the illustrations. The mandible of *E. subfumatus* appears somewhat larger and stronger than that of the other two, and the base is produced into a flange above and behind the fossa of the upper articulation, this flange appearing behind the superior mandibular strut when the whole head skeleton is undisturbed, and being very easily spotted if the mandible be removed. The point of the mandible appears to be more slender and sharper in *D. cavus.* The superior mandibular strut seems longer in this species, and more distinctly right-angled than in *E. subfumatus.* Also the pleurostoma appears stronger and thicker. The spiracles are much the same in size and structure, only the atrium appears more globular in the case of *Eutelus*, with a slightly smaller opening. In each case there are three distinct globular chambers below the atrium ; below the third the top of the stalk itself is swollen, almost making a fourth chamber. The lower part of the stalk develops into a longish, thick-walled swelling, the closing apparatus, below which it suddenly widens out to join the trachea. The atrium is 0·02 mm. in diameter and the whole spiracle is 0·06 mm. long. In *D. cavus* the atrium is 0·023 mm. in diameter.

This is probably one of the most valuable parasites of *D. polytomum* in Europe and its establishment in Canada would be a step of great importance. Its liberation has been advised from the first and 11,500 individuals have been sent from Europe and liberated by 1936.

26. Dibrachys cavus, Walk.

This notorious hyperparasite has been recorded from a long range of Lepidopterous, Hymenopterous, Dipterous and Coleopterous hosts. It is, unfortunately, all too frequently present on *D. polytomum* in Europe, although it has been found acting as both primary and secondary on this host. It has rarely been absent from any sample of cocoons and shows an impartial distribution all over Czechoslovakia. The parasitism is rarely less than 3 or 4 per cent., frequently up to 8 or 10 per cent. of cocoons, though higher figures have not been recorded.

The adults can be distinguished among the other Chalcids as a small dark species, almost black in colour with a metallic blue sheen on the body. The legs and antennae vary from pale to dark brown. The head is markedly carinate, and the antennae inserted fairly low down on the face, but not below the level of the base of the eyes. The abdomen is flattened and longish oval in shape. The wings are clear, with the costal longer than the marginal veins and the post-marginal and stigmal veins equal in length. The size varies from 1·5 to 2·75 mm. in length, depending on the number emerging from a cocoon.

This species is most usually secondary on *D. polytomum*, though it quite often acts in a primary capacity. It attacks practically any of the primary parasites, remains of the larvae of *Exenterus*, *Microcryptus basizonius*, *Lamachus*, *Holocremnus* *ratzeburgi*, and *Hemiteles areator*, having been found in *D. polytomum* cocoons from which *D. cavus* emerged, and of *Torocampus eques* and *Pimpla alternans* in cocoons of *D. sertifer*. A number of eggs are laid in each cocoon, and up to 40 adults have emerged from a single cocoon, though 12 to 15 is the average. The larvae feed externally on the parasite or sawfly prepupa, devouring it completely. The life-cycle is completed in three weeks in summer, with the temperature averaging about 20°C. As parasitized cocoons are available for a longer period in the field than unparasitized, owing to the slower development of the parasite, *D. cavus* can practically always find hosts available from its first appearance in May to its hibernation, as mature larvae, late in September. Thus it can go through 3 or 4 generations in the year in Central Europe.

The mature larva is very similar to that of *Eutelus subfumatus* and the very slight differences in mandibles and spiracles have been described in the section on that parasite and illustrated in figures 18*f* and *g*.

For the sake of the biological control project as a whole, it is to be hoped that this dangerous hyperparasite does not appear in the infested areas in Canada. Its quick life-cycle and fecundity give it a reproductive rate considerably above that of any of the larval parasites it chiefly victimises. In our experience, whole generations of *Holocremnus* and *Lamachus* have been wiped out by hyperparasitism by this species, together with *Hemiteles* and *Leptocryptus*. Dissected sawfly larvae had shown a 10 to 20 per cent. parasitism by larval parasites, whereas cocoons from the same batches produced no adults of these species. It is true that in such cases the total loss of the host through parasitism remains the same, but the effect on slowing down the rate of increase of the primary parasites is obvious.

27. **Diglochys lophyrorum,** Rshka.

The original description of this species by Ruschka and Fulmek (1915) is the only previous record. On this occasion it was bred from *D. pini* cocoons in Bohemia, but the authors do not state whether it was primary or secondary. It was bred from *D. polytomum* cocoons on three or four occasions only during the present work, never more than one or two cocoons in a sample containing this parasite, the percentage being well below 1 per cent.

It is a small, dark insect, most easily confused with *Dibrachys cavus*, being of the same size and colour. The body is dark metallic green, the antennae and legs yellowish brown to dark brown. *Diglochys* can be distinguished from *Dibrachys* by the shape of the abdomen, which is much shorter and round (roundish-oval in male) in contrast to the long, oval abdomen of the latter. The head is large and broad, wider than the thorax, and weakly carinate. Mandibles 4-toothed on each side. The wings are clear, with the marginal vein slightly shorter than the subcostal, and the postmarginal equal to the stigmal.

This species was of too infrequent occurrence for anything definite to be learned of its biology. Judging by the remains in cocoons from which it emerged, it can act as both primary and secondary parasite on *D. polytomum*, and until more information is forthcoming it would be unwise to attempt its introduction into Canada..

28. **Stenomalus sp.**

From a second generation cocoon of *D. polytomum*, collected at Zbiroh, Central Bohemia, in 1932, a dead adult female of an unidentified species of *Stenomalus* was dissected out.

29. **Pleurotropis sp.**

This is recorded as a hyperparasite of various Agromyzid, Coleopterous, and Hymenopterous hosts. One or two isolated examples were bred from *D. polytomum* cocoons from the Brdy Wald and Böhmerwald areas. It is a small, dark metallic green insect, distinguishable from the other parasites by the following points: abdomen relatively small and oval, tarsi 4-segmented, wings clear with very short subcostal vein, broken before joining the long marginal vein, very short radial vein, postmarginal only slightly larger.

Nothing is known of the biology of this Chalcid, except that it is hyperparasitic in the present instance, and for this reason it should be withheld from liberation in Canada.

30. **Microplectron fuscipennis,** Zett.

The biology and importance of *M. fuscipennis* have already been fully dealt with in a previous paper (Morris & Cameron, 1935) and only our more recent observations, together with the repetition of a few important points, will be given here.

During the first three years of the work, this species was not found parasitizing *D. polytomum*, though widely distributed on *D. pini* and *D. sertifier* throughout Europe, becoming a major parasite of *D. sertifer* in the south. The reasons put forward to explain this were: (1) the solitary habits and comparative rarity of *D. polytomum*, which might prevent this parasite from attaining appreciable numbers; (2) the comparative small number of host cocoons that had been collected in the field and examined. In 1935 *M. fuscipennis* was recovered in small numbers (the exact percentage was not ascertained) from cocoons of the first generation of *D. polytomum* collected at Padrt in the Brdy Wald; in 1936, cocoons of this species collected late in the first generation at Hradec in Silesia yielded 12 per cent. of this parasite. In these two years very much larger numbers of cocoons were gathered than at any time previously.

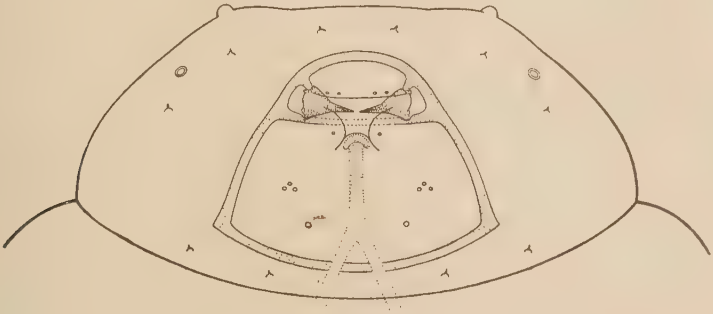


Fig. 19. *Microplectron fuscipennis*: head of mature larva (× 150).

The adults of *M. fuscipennis* are conspicuous because of their dark, clouded wings; general black colour with greenish tinge on head and thorax, and polished bronze abdomen; contrasting white legs; and the marked sexual dimorphism. This latter character is most apparent in the antennae, those of the male being branched, of the female club-shaped. Besides this, the male is smaller, the wings are less clouded, the coxae dark brown, and the abdomen longish oval instead of rotund. The fore-wings of both species are clouded with brown over two-thirds of the distal area with the basal one-third clear. The hind wings are clear. The subcostal and marginal veins are about equal, and the radial longer than the postmarginal.

As with *D. sertifer*, this is really a primary parasite of the sawfly, though occasionally found acting as a secondary on one or other of the Ichneumonid primary parasites. This hyperparasitism was studied in greater detail in the case of *D. sertifer*, and it was considered to be accidental, being really an aspect of multiple parasitism in which the Chalcid was invariably intrinsically superior to the Ichneumonid. The only difference in the biology observed with *D. polytomum* as a host was the smaller number of eggs laid and of adults emerging from the much smaller cocoons of this sawfly. In Silesia the average number of adults per cocoon was only 12. On *D. sertifer* this was found to be 31 in Hungary and 72 in Jugoslavia.

The immature stages are fully described and illustrated in the paper (*loc. cit.*). The eggs can be distinguished from those of *Eutelus*, *Dibrachys*, or *Monodontomerus* by their small size, being only 0·34 mm. by 0·11 mm. The distinctions of the mature larvae of these four species have been mentioned in the section on *Eutelus*. It is only necessary to repeat here the main features of *Microplectron* (fig. 19) : the small mandibles without an upper basal flange, the broad epistoma, and the grouping of the papillae, especially the pair of very large conspicuous papillae lateral to the mouth-parts and in line with the superior mandibular struts, and the two groups of three together on the sub-labial region.

When *M. fuscipennis* was first discovered in numbers parasitizing *D. sertifer* in Hungary in 1934, its value was at once realized and its liberation in Canada advised, and in that year cocoons containing an estimated nine millions of this parasite were sent from Europe. During that winter mass breeding on *D. polytomum* cocoons was started at Farnham House Laboratory, and in the following year this was adopted in the Laboratory at Belleville, and has since been carried on, with the production and liberation of nearly twenty million *Microplectron*, besides which further large shipments of naturally infected *D. sertifer* cocoons have been sent from Europe. The chances of *Microplectron* becoming a really useful controlling factor of *D. polytomum* in Canada are considered pretty good, depending on its tremendous fecundity and rapid rate of increase and the presence of large quantities of readily available host material. The fact that the first recoveries of the insect from Canadian cocoons collected in the field were made in the winter of 1934, only six months after the first liberations, and that it is now well established in many localities, lend strong support to this view.

31. **Sturmia inconspicua**, Meig.

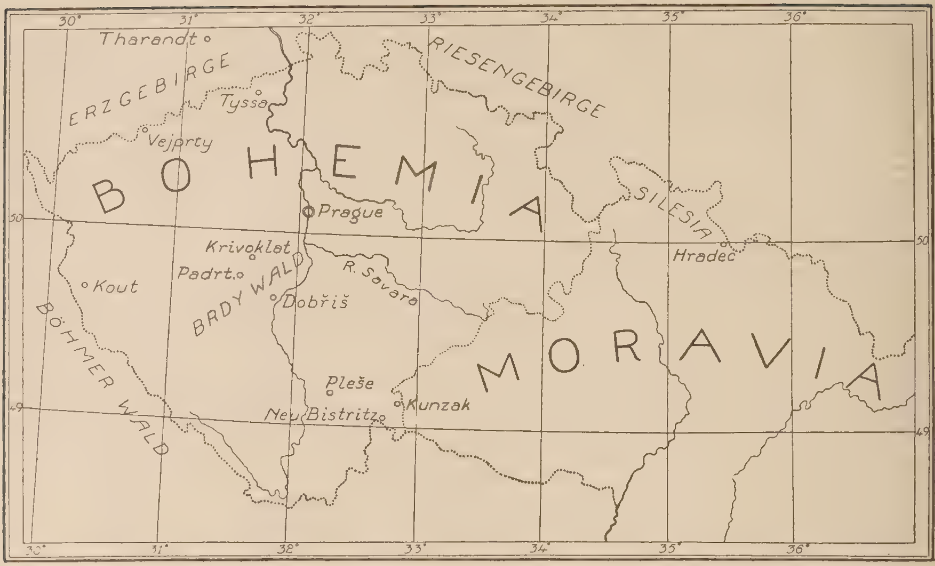
This exceedingly polyphagous Tachinid seems to attack Lepidopterous and Tenthredinid hosts with equal impartiality. Besides many species of Lepidoptera, it has been recorded from the following sawflies : *Diprion frutetorum*, *D. laricis*, *D. pallidum*, *D. pini*, *D. polytomum*, *D. sertifer*, *D. similis*, *D. socius*, and *D. virens*. Baer (1920) records it as a parasite of *D. polytomum* in Germany and gives some interesting notes on its life-history. Sitowski (1925) records it from the same host, among other DIPRIONIDAE, from Poland ; and Webber (1932) gives a full account of the biology of this parasite, which has several times been introduced from Europe into the United States for the control of the Gipsy Moth and *Diprion simile*.

During the present work it was obtained in very small numbers (usually less than 1 per cent. parasitism) from *D. polytomum* at Tharandt in Saxony, Tyssa in the Erzegebirge, and Dobřiš in the Brdy Wald. From *D. sertifer*, however, it was obtained in far greater numbers, showing a 65 per cent. parasitism at Wiener Neustadt in 1934, approximately 5 per cent. at Iszák in Hungary in the same year, and a slightly higher parasitism in the Riesengebirge in 1933 and 1934. In Poland it was common on *D. pini*, reaching 20 to 30 per cent. in 1935 and 1936. A full account and figures of the various stages in the life-history of *Sturmia* will not be given here, as it has been so admirably described by Webber. The following notes, mainly from field observations, are given as being useful for the detection of this parasite and for an understanding of its relationship with its host.

The egg is laid externally on the sawfly larva or prepupa, usually on the side of the thoracic region, and the young larva hatches at once and burrows into its host, where it remains as an internal parasite until fully fed. It then bores a hole out of the empty host skin and pupates within an hour, usually on the ground, lightly buried in the soil or dust, but sometimes on a branch in the neighbourhood of the empty host cocoon. The adults emerge in 3 to 4 weeks. The completion of feeding and emergence of the fully fed *Sturmia* larva takes place, in the majority of cases, after the host has spun its cocoon, but quite often from the dead host larva which has failed in its last ecdysis and spinning. This seems to depend entirely on the age of the larva when it is parasitized. Cocoons from which a *Sturmia* larva has emerged are very easy to recognize, because of the very regular, perfectly round, cleanly cut hole situated exactly at the apex, never slightly eccentric or with jagged edges, as is usually the case with Ichneumonid parasites. The hole is considerably smaller than that made by the emergence of adult sawflies, and slightly smaller than that of most Ichneumonids. Within the cocoon the host skin remains fully distended but completely empty and with a large round hole at one end, most usually posteriorly.

In Central Europe it is usual for *Sturmia inconspicua* to go through several generations in the year. The early generations in spring and summer undergo their development as just described, *i.e.*, the complete life-cycle occupies 5 or 6 weeks. In the last generation in late summer or autumn, however, the primary larva, as soon as it has entered the host, goes into diapause and passes the winter thus, within the sawfly prepupa in its cocoon. In the following spring it devours its host, emerges and pupates within a very short time, and the adults are on the wing in time for the first generation of *Diprion* larvae. A case has occurred, however, in which a *Sturmia* grub, laid on a *D. sertifer* larva in May 1934, went into diapause straight away and did not complete its development or emerge until April 1935. The majority of *Sturmia* of the same generation and from the same host had emerged and pupated in the normal way and given rise to adults in June. These latter must have had alternate hosts, since *D. sertifer* is univoltine. There was a certain number of *D. pini* (bivoltine) in the same infestation and these were heavily parasitized by *Sturmia*, but this host would be no use to the flies emerging in June, as the second generation larvae of *D. pini* were first found in this locality in the middle of August. It seems then that some other hosts, probably Lepidopterous, are necessary for the maintenance of such a strain of *Sturmia*. It is interesting to speculate whether the single generation *Sturmia*, going into diapause as a primary larva in May, is an adaptation to its univoltine host; and whether the presence of the primary larva within the sawfly prepupa inhibits the latter's metamorphosis in September (the emergence time for *D. sertifer*) in order to make this method of overwintering possible. Alternatively, it is possible that the rate of development of the parasite is influenced by that of its host, and that the only *Sturmia* larvae that will survive are those in the small proportion of *D. sertifer* larvae that go into diapause over the winter.

In considering the chances of survival of this species in Canada it must be realized that the biology of *D. polytomum* there is slightly different. Over a very large portion of the infested area in the Gaspé Peninsula, the sawfly is univoltine, with a very prolonged feeding period, from about June to August. At slightly lower levels there are two generations almost merged into one, through prolongation of the first generation's feeding period and irregular emergence of adults. Only on the lowest ground, in New Brunswick, are there two very distinct generations. Thus the requisite conditions do prevail in which *Sturmia* could find an almost continuous supply of hosts through the short summer. The Gaspé would be the best area for liberation of the races from *D. sertifer*. The lower areas would perhaps be more suitable for those coming from *D. pini* and *D. polytomum* in Europe. In parts of Poland, where the winter climate is very severe, *S. inconspicua* is undoubtedly a major controlling agent on bivoltine *D. pini*, so there are the opportunities and possibilities of its becoming an important check on *D. polytomum* in Canada. The ability for acclimatisation has already been proved by its recovery from indigenous cocoons in Canada.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BRDY WALD
Dobřiš
R. Sazava
BÖHMER WALD
MORAVIA
Pleše
Kunzak
Neu Bistritz
50
49

Fig. 20. Map showing the chief collecting centres in Czechoslovakia.

32. Key to the Parasites of Dipron polytomum.

1.—Dipterous .... *Sturmia inconspicua.*
Hymenopterous 2

2.—Wingless 3
Winged 4

3.—Species 4·3 mm. or longer, excluding ovipositor ; head black, thorax and first three abdominal segments red .... *Gelis acarorum.*
Species only 3 mm. long ; head and abdomen, except for first segment, black ; thorax reddish-brown with metanotum black, petiole light brown... *Gelis* sp.

4.—Wings rudimentary, not extending beyond the metathorax .... *Spilocryptus abbreviator.*
Wings fully developed 5

5.—Wings with well-developed venation, antennae not elbowed 6
Wings with rudimentary venation, antennae elbowed 22

6.—Wings with one recurrent nervure .... *Microbracon* sp.
Wings with two recurrent nervures 7

7.—Forewings with three transverse dusky areas .... *Hemiteles areator.*
Forewings without transverse dusky areas 8

8.—Hind tibiae without spurs 9
Hind tibiae with spurs 12

9.—Keel on front margin of mesosternum ; first two abdominal segments broadly banded with yellow .... *Exenterus marginatorius.*
Not as above 10

10.—Apical segments of abdomen ventrally red ; last ventral segment in ♀ long and acute ; front and middle legs yellow, only femora marked with black...... *Exenterus tricolor.*
Apical segments of abdomen ventrally not red ; last ventral segment of ♀ obtuse ; front tibiae usually marked with fuscous 11

11.—Front and mid coxae black, yellow beneath ; yellow tarsi ; hind coxae black ; propodeon less conspicuously yellow marked ; last abdominal segment in female very obtusely angled (fig. 13*b*)………………….*Exenterus adspersus.*
Mid coxae almost or entirely yellow, hind coxae yellow, black above ; propodeon more conspicuously yellow marked ; last abdominal segment in ♀ almost right-angled (fig. 13*c*)……………………………………………*Exenterus* sp.

12.—Areolet present, well defined but with outer side wanting………………………13
Areolet present or entirely wanting ; when present always closed……………14

13.—Ridges of metathoracic areolation strong ; abdomen entirely black…………… *Hemiteles sordipes.*
Ridges of metathoracic areolation weak ; abdomen almost yellowish-red, except for petiole and sides of segments 2 and 3, which are black……….. *Leptocryptus aereus.*

14.—Areolet distinctly pentagonal……………………………………………………15
Areolet quadrate, triangular, or wanting…………………………………………16

15.—Body entirely black ; antennae black, usually with white spot in middle segments above………………………………………*Habrocryptus polytomi.*
Middle segments of abdomen red, white ring in middle of antennae…………… *Microcryptus basizonius.*

16.—Abdomen dorsally depressed and broadly sessile ; areolet small and quadrate ; ♀ with ovipositor at least one-third length of abdomen……………………17
Abdomen petiolate ; areolet triangular, quadrate or wanting…………………18

17.—Metathoracic areolation absent, only vestiges of the two long ; ovipositor only one-third length of abdomen……………………*Pimpla* (*Itoplectis*) *alternans.*
Metathoracic areolation partly developed, with completely enclosed area superomedia and area posteriomedia ; ovipositor only half length of abdomen ……………………………………………………*Delomerista* sp.

18.—Areolet large and quadrate, thorax and abdomen shining and slender………19
Areolet small, quadrate, triangular, or wanting ; thorax matt………………20

19.—Head, thorax, and abdomen mainly black, except for reddish spot in centre of thorax and median segments of abdomen light brown……………………… *Mesochorus thoracicus.*
Head, thorax and abdomen entirely light reddish-brown *Mesochorus fulgurans.*

20.—Areolet small, usually distinctly quadrate, rarely almost triangular ; thorax and abdomen dull black ; tegulae only yellow…………*Holocremnus ratzeburgi.*
Areolet wanting or small and triangular ; face and thorax beneath yellow, black above, with front edge of scutellum and tegulae yellow……………………21

21.—Face of ♀ entirely yellow, or with large yellow patch ; hind femora red, tibiae distally black and tarsi entirely black ; abdominal segments with light posterior margin…………………………………………………*Lamachus* sp.
Face of ♀ usually black, or with small yellow patch ; hind legs, except for coxa, black, or clouded with black ; posterior margins to abdominal segments less markedly light ; only ♀ obtained…………………*Lamachus spectabilis.*

22.—Female with exserted ovipositor…………………………*Monodontomerus dentipes.*
Female without exserted ovipositor………………………………………………23

23.—Wings distinctly clouded with dark brown ; antennae of ♀ spindle-shaped, of ♂ filiform with three short branches from segments 2, 3, and 4 of flagellum…… *Microplectron fuscipennis.*
Wings clear, antennae of ♂ and ♀ similar………………………………………24

24.—Tarsi 4-segmented ; marginal nerve longer than subcostal……*Pleurotropis* sp.
Tarsi 5-segmented ; marginal nerve shorter than subcostal……………………25

25.—Postmarginal vein of same length as stigmal (radial) ; occiput carinated......26

Postmarginal vein longer than stigmal ; occiput never carinated...............27

26.—Occiput markedly carinated ; abdomen longish oval...........*Dibrachys cavus.*

Occiput weakly carinated ; abdomen round, in ♂ round oval.................... *Diglochys lophyrorum.*

27.—Antennae inserted at base of face (below an imaginary line drawn from base of eyes) ; clypeus without median tooth at apex...........*Eutelus subfumatus.*

Antennae not inserted at base of face ; clypeus at apex armed with a median tooth or with four equally well-developed teeth................................28

28.—First joint of antennae not longer than pedicel ; clypeus with four well-developed teeth ; abdomen sharply pointed and keeled ; a large species, dark metallic green tinged with bronze..........................*Habrocytus* sp.

Pedicel much longer than any antennal joint ; clypeus at apex with median tooth ....*Stenomalus* sp.

33. Key to the Mature Larvae of the Primary Parasites.

1.—Dipterous larvae emerging from host cocoon before pupation.................... *Sturmia inconspicua.*

Hymenopterous larvae pupating in host cocoon......................................2

2.—Large larvae between 4 and 9 mm. long, Ichneumonid-type head skeleton ; usually solitary...3

Small larvae, less than 4 mm. long ; Chalcid-type head skeleton ; usually gregarious 11

3.—Labial ring broken basally ; hypostoma elbowed ; spiracles small, atrium 0·02 mm. diameter, and without closing apparatus ; large dark-brown eggs, 1 mm. long, always found in host skin..........................*Lamachus* spp.

Labial ring complete ; hypostoma regularly curved or wanting ; spiracles large and with closing apparatus, atrium more than 0·02 mm. diameter, except in *Holocremnus* and *Delomerista* ; eggs not found in host skin, except *Holocremnus*...4

4.—Labial ring drawn out ventrally, giving it a keyhole shape ; Y-shaped pigmented area in labial ring divides lower part into two lobes ; spiracles minute, loaf-shaped, at most 0·025 mm. long, no closing apparatus ; dark brown egg 0·8 mm. long, always found in host skin...........*Holocremnus ratzeburgi.*

Labial ring horseshoe-shaped, at most thickened basally ; labial area not divided by pigmented Y-shaped strip ; spiracles at least 0·06 mm. long or longer, with closing apparatus ; eggs not found in host skin..................5

5.—Hypostoma wanting ; labial struts mere vestiges ; labial ring with broad, thickened, rather flattened base ; spiracles with broad atrium, 0·045 mm. wide, lined with inwardly projecting spines ; no cocoon spun.............. *Pimpla alternans.*

Hypostoma present ; labial struts developed ; spiracles with atrium less than 0·04 mm. wide with no internal projections ; white papery cocoon spun...6

6.—Slightly hairy appearance, through hairs 0·1 mm. long sparsely scattered on body ; labial ring thickened and flattened basally, labial struts somewhat reduced ; spiracles small, atrium 0·02 mm. diameter.........*Delomerista* sp.

Larva of smooth appearance ; if spiracles present never more than 0·035 mm. long ; labial ring not flattened or markedly thickened basally ; labial struts well developed ; spiracles large, atrium at least 0·03 mm. diameter . . 7

7.—Clypeal arch absent ; epistoma complete ; mandibles small, slender pointed, without bristles ; ligula absent ; salivary opening unchitinized ; skin closely covered with fine slender setae, 0·024 mm. long, giving downy appearance under low power.................................*Exenterus* spp.

Clypeal arch present ; epistoma usually incomplete ; mandibles broadly triangular, armed with bristles ; ligula present ; salivary opening usually chitinized ; skin covered with very small papillae or spinules and occasional stiff setae 8

8.—Clypeal arch rounded ; epistoma almost complete ; labial struts right-angled ; spiracle with reticulate thickening to atrium......*Spilocryptus abbreviator.*

Clypeal arch flattened ; epistoma distinctly incomplete ; labial struts only slightly curved ; spiracles with annular thickening to atrium 9

9.—Opening to salivary duct strongly chitinized ; mandibles with broad strong points ; spiracles with very short stalk ; skin armed with blunt, conical spinules...*Microcryptus basizonius.*

Opening to salivary duct very weakly chitinized ; mandibles with rather more slender points ; spiracles with long stalk......................................10

10.—Epistoma hardly developed at all ; ligula small, V-shaped ; spiracle of average size, 0·07 mm. long ; skin armed with slender, sharply conical spinules......... *Habrocryptus polytomi.*

Epistoma slightly developed ; ligula large, Y-shaped ; spiracle with very long stalk, total length 0·1 mm., skin with small, rounded papillae.............. *Hemiteles* spp.

11.—Larvae hairy ; pupa of female with long ovipositor recurved over back ; egg-shells 0·7 mm. long present in cocoon..............*Monodontomerus dentipes.*

Larvae smooth ; pupae without projecting ovipositor ; egg-shells in cocoon 0·45 mm. long or less..12

12.—Epistoma broad and flattened ; tentorium uniformly curved dorsally ; a pair of large papillae on face, one each side of mouth in line with superior mandibular struts ; eggs 0·34 mm. long....................*Microplectron fuscipennis.*

Epistoma narrow and rounded ; tentorium abruptly arched dorsally in the middle ; papillae on face all small and of equal size ; eggs 0·45 mm. long...13

13.—Base of mandibles with flange above and behind superior fossa ; spiracle with more globular atrium, approximately 0·02 mm. diameter.................... *Eutelus subfumatus.*

Mandibles without any basal flange ; spiracle with atrium rather flattened, approximately 0·023 mm. diameter, with larger opening.....*Dibrachys cavus.*

34. Summary.

A severe outbreak of the Spruce Sawfly (*Diprion polytomum*, Htg.) in Eastern Canada led to a request to Farnham House Laboratory to investigate, and if possible collect and export, the parasites of this insect in its native home in Europe.

Work started in 1932 and it was found that *D. polytomum* was a comparatively rare insect in Europe, though widely distributed. It is heavily parasitized, 31 species of Hymenopterous and Dipterous parasites having been found up to the present. Nearly twenty-eight million parasitized cocoons and eggs of this and other species of *Diprion* have been collected and despatched from Europe, and work is still continuing.

Previous to the present work only 13 species of parasites, a list of which is given, were recorded from this host.

Of the 31 species now known, 15 are primary, 5 can be primary or secondary, and 9 secondary only ; in 2 cases the status is not known.

Descriptions of all the species are given and in the case of the obligatory and facultative primaries, the biology and immature stages are also described and notes added on their suitability for introduction into Canada. A key to the adult parasites is given, and a key to the larval stages of the primary and facultative primary parasites. Some practical notes are also given, including methods of accelerating the emergence of parasites in winter and methods of preparing parasite larvae for examination and identification.

35. Acknowledgments.

It is with great pleasure that we take this opportunity of expressing our indebtedness to the many who have helped us during the progress of this work. Especially, we should like to thank Dr. W. R. Thompson, F.R.S., the Superintendent of Farnham House Laboratory, for his invaluable and unfailing advice and sympathy, which have done so much to help us overcome the many difficulties involved. Also we are deeply indebted to Sir Guy A. K. Marshall for his valuable aid in bringing about friendly relations with the various countries in which we worked, and to Dr. C. Ferrière and Mr. J. Perkins for the identifications of the parasites ; to Dr. Arthur Gibson, Dominion Entomologist of Canada, we owe our gratitude for making this work possible and for enlisting the support of the Canadian Government and Forest Associations ; and to Mr. A. B. Baird and his staff at Belleville for their co-operation and reports. Finally, we should like to express our thanks to Mr. R. J. Spittle for the able way in which he has helped us with the preparation of the illustrations, and to Mr. R. C. Jeffery for his ready response to the many and urgent demands made on the Laboratory during the course of the work on the Continent and for his help in preparing this paper for the press.

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TSETSE-FLIES IN THE OL OROKUTI AREA OF THE MASAI RESERVE, KENYA COLONY.

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An investigation of the " fly-belts " in the Ol Orokuti area of the Masai Reserve was carried out early in April 1934, in response to a request from the European farmers of the Sotik district.

The recommendation by the Kenya Land Commission (1933) to allot the major portion of the Chepalungu Forest area to the Wa-dorobo and the Lumbwa (Kipigis) native tribes aroused the fear, among the farmers, that the occupation of the forest by herds of native cattle would serve to attract the tsetses from the Masai Reserve to the vicinity of the " settler " farms, and thus expose their stock to infection with trypanosomiasis. It appears that the European farmers of Sotik contemplated the introduction of a dairy industry scheme to the district.

Certain farmers, well acquainted with the Chepalungu Forest and the surrounding country, believed that the tsetses were steadily advancing up the Mara and the Mogor Rivers towards the Chepalungu Forest. and that this advance presented a very real danger to further development. Some farmers feared that the tsetses had already reached the forest, and maintained that they had certainly arrived at the junction of the Mara and the Nyangoris Rivers. Apparently, it had been proposed to settle the Wa-dorobo between the junction of these two rivers; and to allot the area not occupied by the transferred Wa-dorobo to the Lumbwa. Another portion of land, approximately 8,800 acres on the west of the Chepalungu Forest, had been demarcated for addition to European settlement. Insufficient water-supply, and the proximity of native cattle which might become infected with trypanosomiasis, impaired the attractiveness of this area of good grazing land.

The Chepalungu covers an area of about 164 square miles. The greater part is outside, and to the north, of the Masai boundary, extending from Gelegele to near the junction of the Mara and the Nyangoris Rivers ; it is continuous, on the east of the Mara, with the dense thickets extending to the Nasiandet River. To the south of the Reserve boundary, the forest stretches into Ol Orokuti, where it breaks up into an irregular network formed by riverine vegetation and clumps of thickets interspersed with open glades of different dimensions, and patches of Acacia savannah.

Juniperus procera (Mutarakwa), the common cedar, is found in parts of the Chepalungu. The dominant trees and the thicket-forming plants in the forest, and along the course of the Mogor and several other streams in Ol Orokuti, are :— *Olea chrysophylla* (Mutamaiyu), the brown olive ; *Elaedendron* sp. (Mutanga) ; *Celtis Krausiana* (Murundu) ; *Warburgia ugandensis* (Mugiga) ; *Tecla viridis* (Munderendu) ; *Olea Hochstetteri* (Musharage) ; *Cassipourea Elliottii* (Musaisi) ; *Euclea lanceolata* (Mukinye) ; *Schrebera alata* (Mutoma) ; *Maba abyssinica* (Muirosi) ; *Ochna Stuhlmannii* (Mungarima) ; *Trichocladus malosanus* (Mwaio), the wych hazel ; *Calodendron capense* (Muroroa), the Cape chestnut ; and *Polyscias ferruginea* (Mutati).

Trichocladus malosanus is extremely abundant ; its multiple, liana-like branches provide a convenient framework or support for creeping plants and for shrubs to form dense and sheltered canopies. *Acacia* species are scattered unevenly throughout and are usually found on the fringes of the forest, and in the more open country of the Masai Reserve.

In the Chepalungu there are extensive seasonal swamps ; and there are numerous open spaces with grazing much coveted by the cattle-owning tribes of the neighbourhood. The river courses in the forest are said to be dry for several months in the year, but at the time of the investigation there was a heavy flow of water in the streams running into the Mogor.

No tsetse-flies were found in the forest which was carefully searched. *Haematopota* and other TABANIDAE were numerous in swampy areas.

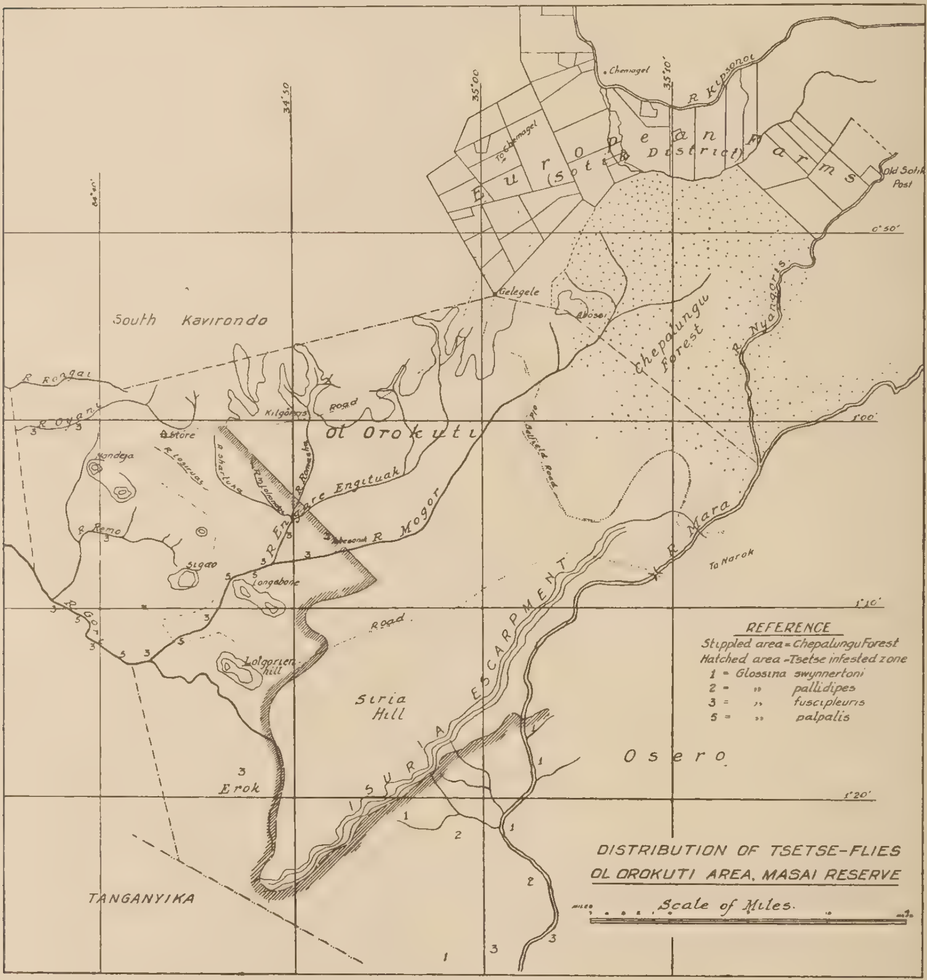
34°30
35°00
35°10'
0°50'
1°00'
1°10'
1°20'
European Farms (Sotik District)
To Chemagel
Chemagel
R. Kipsonoi
Old Sotik Post
Gelegele
Abosei
Chepalungu Forest
R. Nyangores
South Kavirondo
R. Rongai
R. Oyani
Store
Kilgoris
Road
Ol Orokuti
Kandeja
R. Logituas
R. Sharlung
R. Kimjolonik
R. Romosha
R. Engare Engituak
R. Mogor
R. Remo
Sigao
Longabone
R. Gori
Lolgorien hill
Road
Siria Hill
Erok
SIRIA ESCARPMENT
R. Mara
To Narok
Osero
TANGANYIKA
REFERENCE
Stippled area = Chepalungu Forest
Hatched area = Tsetse infested zone
1 = Glossina swynnertoni
2 = ,, pallidipes
3 = ,, fuscipleuris
5 = ,, palpalis
DISTRIBUTION OF TSETSE-FLIES
OL OROKUTI AREA, MASAI RESERVE
Scale of Miles.

Fig. 1.

Natives (Masai, Lumbwa and Dorobo) who frequently trekked through the forest, and some of whom grazed their cattle in the glades, strongly maintained that they knew that tsetses were present in the Masai Reserve ; and they were certain that the fly had not spread further than a point in the Kilgorris area. The Lumbwa have no specific native name for a tsetse-fly ; they speak of most biting-flies (including the mosquito) as " Kalyangat " ; they use that name for a tsetse also ; *Haematopota* and *Tabanus* are known to the Lumbwa as " Soguriet."

The investigation was now extended into the Masai Reserve. A wide strip of country below the boundary is occupied by the Uasin Gishu Masai who have recently been moved into the area. These people, with their herds of cattle, utilize the zone from Gelegele to near Kilgorris—on the west of the Mogor ; they appear to have been informed of the presence of tsetses along some of the streams near Kilgorris, at two or three salt-licks, and along part of the Mogor ; and they stated that their own observations confirmed the information given them by other natives. The Uasin Gishu Masai, therefore, confine their cattle to the hills in the northern section of this district.

Continuing the journey into Ol Orokuti by the Chemagel-Lolgorien road, it was possible to pitch camp, and then penetrate the country to the east in search of tsetses. Ultimately reaching the Shartuka (Asurto) stream, a special effort was made, with the assistance of some local natives, to find tsetses, which were reputed by Europeans and natives to infest the bush along the stream. None was found after three days' search. A little lower down, however, on the Engare Engituak stream the first tsetse, *Glossina fuscipleuris*, was collected. The Shartuka flows into the Engare Engituak, and it seems not unreasonable to suppose that the tsetse spreads up the Shartuka in favourable seasons. Furthermore, specimens of this species of fly were caught on the Loliondoi, another tributary of the Engare Engituak. No tsetses were found on the Romasha River, but several were collected at the salt-lick, Tebesonik, between Engare Engituak and the Mogor Rivers. No tsetses were found on the Mogor until a point was reached about four and a half miles above its junction with the Engare Engituak. From this point downstream the species was common. Another species of tsetse was encountered on the Mogor half-way between Longabone hill and the Engare Engituak. This species—*Glossina palpalis*—appeared to be more abundant than *G. fuscipleuris*, which also occurred in the same belt. The mixed fly-belt extended to and along the Gori River, which forms the boundary between the Masai Reserve and the Watende country. *G. palpalis* only was found on the Oyani (Kayan) River near the Masai-South Kavirondo border ; and *G. fuscipleuris* only on the Remo or Tangalasha stream. Although the natives claimed that the larger fly (*G. fuscipleuris*) was to be found on the Losiruai stream, no specimens were collected there.

As a result of this investigation, the tsetse-infested area may be defined by a line drawn from a point on the Chemagel-Lolgorien road, three miles east of the store marked on the map and where the Shartuka crosses the road, to the Mogor, a short distance above the Tebesonik salt-lick ; thence across the Mogor River to a distance two miles south of that river ; thence in a westerly and south-westerly direction parallel to the Mogor as far as a point south-east of Longabone hill. The Siria hills lie to the south and south-east of this belt, and as they are free from infestation they form a break in what might otherwise have been a continuous, broad fly-belt from Ol Orokuti to trans-Mara, where *G. pallidipes*, *G. fuscipleuris* and *G. swynnertoni* exist. On a former visit one was informed by the natives that the tsetses spread over the country from Lolgorien to Erok, and that the flies extended from trans-Mara to the Engarare, thence to Erok (Osinandei stream) and to Lolgorien. A solitary *G. fuscipleuris* was captured in the forest (at about 5,900 feet) on the slopes of the Siria hills during that visit (Lewis, 1934). It seems, therefore, that there is a possible linking of the two belts, but that the Siria hills form a barrier to a connection along a broad front. In an account of the tsetse-flies in the Masai Reserve published in 1934, the author stated that Ol Orokuti was uninhabited mainly because of its infestation by *G. pallidipes* or *G. palpalis*—both species being known to the Masai as Endorrobo maibor. During that investigation it was not possible to cover the whole of Ol Orokuti. It is now evident that the tsetses infesting the area, north and west of the Mogor, are *G. palpalis* and *G. fuscipleuris*.

The area which has been defined, and which is shown on the appended map, cannot be considered as an entire permanently fly-infested zone. There are patches of open country which are, in themselves, free from fly. They are, however, unsafe for cattle as tsetses spread into them during favourable seasons ; and some of the flies remain in the adjacent bush even when adverse conditions have set in.

Having mentioned the store on the Lolgorien-Chemagel road, it should be explained that the store serves as a significant landmark in that it is used as a station for the changing-over of transport by oxen, from the Sotik (or Chemagel) side to transport by lorries or motor-cars from the store to the Lolgorien gold-mines. This " change-over " routine was adopted because oxen used from the store to Lolgorien frequently contracted trypanosomiasis and died. *G. fuscipleuris* was collected on two occasions from lorries conveying goods from Lolgorien to this store. The flies were obviously attracted to the moving vehicle between 8 a.m. and 10 a.m. It is not known to what extent fast-moving vehicles attract this species of tsetse, nor is it known to what distance from their haunts the flies may thus be carried, but it is indicated that given favourable conditions at the point where the flies alight from the vehicles, other foci of infestation may be created.

It was hoped that the development of the gold-mines in the Lolgorien area would provide a market for produce grown in the Sotik district, and, no doubt, speedy mechanical transport would be utilized for the purpose. The hope has not fully materialised, thus relieving to some extent what would otherwise have been a serious danger of extending the fly-infested zone, and rendering unsafe for cattle the locality which has recently been allocated to the Uasin Gishu Masai and forcing these people nearer and nearer to the Chepalungu Forest. Before dealing with other aspects of this investigation, it will be convenient to revert to another reputed source of danger of fly extension to the Chepalungu Forest, namely the courses of the Mara and the Nyangoris Rivers. It has been stated (Lewis, 1934) that tsetse-flies do not appear to have spread along the Mara as far north as its junction with the Safaringo ; and that the Tusiek stream (running into the Mara from the eastern side) marks the northern limit of the fly-zone in this locality. Several searches were made down the Nyangoris and the Mara to ascertain whether one or more isolated " pockets " of fly had escaped attention. No tsetses were found.

The present position is that there is no evidence to support the belief that tsetse-flies are steadily advancing along the Mara and the Mogor Rivers towards the Chepalungu Forest. The infested belts do not appear to have extended since the last investigation was carried out. The area north and north-west of the Mogor had not previously been surveyed. *G. fuscipleuris* is more widely distributed in Ol Orokuti than was hitherto known ; and the presence of *G. palpalis* on the Kayan River has been confirmed. There are indications that one (or both) species is responsible for the transmission of animal trypanosomiasis. The natives of the district are most reluctant to utilize the excellent grazing in the fly-infested area because of infection from animal trypanosomes and as a result of mortality among cattle which has been experienced. The movement of additional stock into the areas bordering on the fly-zones, and an increase of traffic on the Lolgorien-Chemagel road, might possibly induce and assist the spread of tsetses, unless some precautionary measures are adopted.

Investigations into the incidence of tsetses in a given area frequently have as their primary objective the solution of administrative problems of immediate significance. A detailed study of the bionomics of the flies may not be practicable in such cases, and the investigator must rely, for his practical recommendations, on the local findings, on his wider experience with the pests in his particular country, and on the relative information obtained from the results of his colleagues in other territories. Nevertheless, he will always be able to make observations which, when recorded, may add to the knowledge of a particular species.

G. fuscipleuris has not received as much attention as many of the other species of tsetses ; it has been found in widely separated localities and in different countries ;

but it has hardly ever been reported to occur in large numbers: Apart from the record for the Sonjo Valley (Tanganyika) by McCall (1927 ?) and the isolated record of the species in the Buganda Province (Uganda) in the Annual Report of the Veterinary Department (1935), there is no evidence of its occurrence in a pure *fuscipleuris* fly-belt ; and the species has not been incriminated in the transmission of trypanosomiasis.

G. fuscipleuris was described by Austen (1911) from a specimen collected in the Ituri Forest, north-eastern Belgian Congo. Subsequently it was found in other parts of the Belgian Congo. Gerard (1920) captured the fly in the mining region of the Upper Lukuga, between 9 a.m. and 12 noon, on little brooks, partly dried up, flowing between banks covered with a belt of luxuriant forest. Newstead (1924) gives a number of localities from which *G. fuscipleuris* has been collected in the Belgian Congo. Schwetz (1931, 1933) found the species to be rare in the eastern border of the Province Orientale (Congo Belge) and in the plain region south of Lake Edward. Later (1934) he failed to obtain specimens in the Ituri Forest, but states, in view of the previous record, the fly appears to be extremely rare. In Uganda, *G. fuscipleuris* is mainly found in the Western Province on the east of Lake Edward, and on the eastern and northern borders of Lake George ; it has also been collected at the foot of Ruwenzori in the Toro district (Western Province) ; and in the Mubende district (Buganda Province) about twenty-five miles east of Lake Albert. King (1924) reported *G. fuscipleuris* from the Sudan, and Bedford (1930) collected specimens in the Tembura and Meridi districts. In Kenya Colony, Woosnam discovered this fly on the Enderrit River, in the Masai Reserve ; and, more recently (1934), the writer found it to be common along the Enderrit, Mara and Mogor Rivers.

It is not clear, from the literature available, whether *G. fuscipleuris* in the Belgian Congo is always found with other species of tsetses. A collection of tsetses sent from the Kibali River and its tributaries in the gold-mining area of Kilomoto (to the east of the West Nile Province, Uganda) of Belgian Congo, contained several *G. fuscipleuris* and numerous *G. palpalis*. A map giving the distribution of tsetses in Uganda shows that, with the exception already referred to, *G. fuscipleuris* exists in mixed fly-belts, and inhabits areas where *G. palpalis*, *G. pallidipes* and *G. morsitans* also are present. Bedford (1930) shows that where *G. fuscipleuris* is found, there are also *G. palpalis*, *G. morsitans* and *G. fusca*. In Kenya it has been shown that *G. fuscipleuris*, *G. swynnertoni*, and *G. pallidipes* were taken in a mixed fly-belt on the Mara River, and that *G. palpalis* and *G. fuscipleuris* were found together on the Mogor River.

Observations on the tsetses in Ol Orokuti have shown that both *G. fuscipleuris* and *G. palpalis* are common along the Gori River from its junction with the Mogor to where it crosses the Reserve boundary into Southern Kavirondo. *G. pallidipes* was not found in Ol Orokuti, but the writer is informed by Mr. Symes, Medical Entomologist, who is well acquainted with the tsetses in South Kavirondo, that *G. pallidipes* is fairly abundant in the triangle formed by the Gori and the Kuja Rivers in South Kavirondo. This belt of *pallidipes* is many miles away from the Masai Reserve, but the numerous streams and rivers in the district may serve as possible lines for the seasonal dispersal of the species—and a possible source of infection of trypanosomiasis to Masai cattle which are sometimes found near the border.

In all other localities of Ol Orokuti where *G. fuscipleuris* was found, other species of tsetses appeared to be absent. This species was most abundant in the dense bush along the larger rivers. The vegetation comprised those plants which have been mentioned earlier in this paper. Even during the brightest time of the day there was deep shade in the bush, the undergrowth was frequently very dense, and the atmosphere extremely humid. Apparently the flies in this belt migrate up the tributaries of the large rivers in favourable seasons, and remain in small isolated pockets of bush when adverse conditions set in. The Engare Engituak was a flowing river when the investigation was undertaken ; it harboured less flies than the Mogor, but more flies than the Loliondoi and the Remo, which contained only a few puddles of water. The salt-licks were near the large rivers, and the *fuscipleuris* caught at the licks were attracted from the surrounding clumps of thicket. Many of the specimens collected were found when searching along game paths over which the dense bush grew to form a sort of tunnel ; and in practically every other instance there was either an open, treeless glade, or an open Acacia forest fairly near. The Acacia was largely, *A. seyal*.

From the observations made, it appears that *G. fuscipleuris* prefers the dense vegetation of the large, flowing rivers. It occurs in such similar haunts as *G. palpalis*, and in dense bush on the Mogor where *G. palpalis* has not yet penetrated. It seems less dependent for its existence upon such conditions than *G. palpalis*, and shows a greater tendency to spread further afield and remain in scattered patches of bush, and at the head of small river basins. On the tributaries of the Kibali River in Belgian Congo, *G. fuscipleuris* appears to be found most frequently on the upper reaches, and at the head-waters. In some cases (Aru River) it inhabits the lower reaches with *G. palpalis*—conditions somewhat similar to those in Ol Orokuti.

Like several other species of tsetses the primary home of *G. fuscipleuris* is in the vicinity of water ; unlike *G. pallidipes* and *G. swynnertoni* in the Masai Reserve, it does not range over open country in search of food, but rather waits in ambush, as it were, in shaded places, and dashes to attack animals which pass near its hiding-place. It does not appear to be an active fly, and is not readily attracted to man. On the other hand, it is a determined species, the flies encountered making a sudden attack and beginning to feed immediately. There is no hovering about, no signs of excitement, before piercing the host, as is often seen with *G. palpalis*, for instance. While it cannot be said that *G. fuscipleuris* is shy of man, it undoubtedly prefers cattle or game, especially large game frequenting the forest and dense bush. It readily attacks cattle, making herds at a salt-lick extremely restless, and in some cases causing them to stampede. Its flight is heavy, but it is certainly swift for the short distances it appears to travel.

G. fuscipleuris was found to be most active in the morning. Numerous specimens were collected on the Mogor and Mara Rivers from 7.30 a.m. to about 2 p.m., when native herds of cattle were watering at the rivers. When disturbed in the bush, even at later hours, the flies will attack man or beast ; and it has been shown that flies are attracted to and carried by motor-vehicles. While searching on the banks of the Mogor, it was observed that *G. palpalis* came to the fly-boys and the screen when the boys were moving slowly up and down the river at a fairly open spot, whereas *G. fuscipleuris* appeared only when the boys approached a clump of bush throwing a dense shade across the river. *G. palpalis* was attracted to the screen as well as to the boys, but *G. fuscipleuris* invariably attacked the boys only.

The average altitude at which *G. fuscipleuris* is most abundant in this area is 4,800 feet, the range being from 4,600 feet to about 5,400 feet. It is not uncommon at 5,600 feet, and it will be recalled that one specimen was taken on the Siria hills at about 5,900 feet.

As a matter of routine on a field investigation of this nature, an endeavour is always made to locate breeding-places of tsetses. An area adjacent to a permanent fly-belt may be infested only for a short period, and when examined may be entirely free from fly. A few pupae or puparia shells may be discovered to confirm reports made by natives or Europeans. On a few occasions, the finding of empty puparia has verified the statements made which could not be supported by the discovery of adult flies outside the permanent fly-belt ; and these temporary breeding-places have enabled the investigator to define more correctly the area dangerous to stock.

On the other hand, it is seldom possible to make prolonged searches for breeding-grounds, and it is necessary, in the circumstances, only to ascertain the major, practical points with regard to tsetses in the area.

A few pupae of *G. palpalis* were collected in the heavily infested area of the Mogor; but searches for pupae of *G. fuscipleuris* were unsuccessful.

The fly-infested area between the Mogor River and the Chemagel-Lolgorien road is uninhabited and devoid of stock. The Masai who dwell on the Siria hills, and the Purko tribesmen, who periodically cross the Mara to graze their cattle below the Chepalungu Forest between the Mogor and the Mara, take their stock to water at the Mogor in the dry seasons. Deaths from trypanosomiasis are not infrequent according to the natives, but it is not known which species of trypanosome is responsible for the mortality. It is known that when oxen were used for transport to and from the Lolgorien gold-mines, infection by *Trypanosoma vivax* was common; and in some cases *T. congolense* was identified in blood smears from sick oxen.

In the vicinity of Kilgorris, and between it and the South Kavirondo border, there are many herds of cattle; they move to the region of the Rongai River, and are sometimes found between the Rongai and the Kayan. These herds usually concentrate near Kilgorris. Recently (in 1933) the Uasin Gishu Masai were moved into Ol Orokuti. They were advised of the presence of tsetses and soon learned to keep their cattle at a safe distance from the fly-zone already defined. A native elder who had lived in Ol Orokuti for very many years informed me that the flies have gradually spread from the Gori to and up the Mogor and have extended over a large area in the course of many years. He showed me where his old cattle kraals and villages had been, and took me to a series of these, stating how he had been compelled to retreat before the advancing tsetses. Similar evidence was given by other natives.

Blood smears from diseased cattle at Kilgorris have been known to contain *T. congolense* and *T. vivax*. The former species was found also in cattle from the Oyani or Kayan River.

What species of tsetses are responsible for these infections it is impossible to state. *G. palpalis* may account for *T. vivax* and, more rarely, for *T. congolense*; *G. pallidipes* spreading from the Kuja may convey *T. congolense* near the Oyani; but it seems that although *G. fuscipleuris* cannot definitely be incriminated in the transmission of animal trypanosomes, the fact that the natives will not occupy the area, where apparently this species alone exists, is a reason for associating it with the disease.

At interviews with the European farmers residing near the Chepalungu Forest, it was stated that animal trypanosomiasis was not restricted to the Masai Reserve. Not infrequently cattle as far even as Kericho harboured trypanosomes and the opinion was expressed that biting-flies (*Stomoxys*, *Haematopota* and *Tabanus*) might be responsible for the spread of the disease. The presence of the trypanosomes in the blood-smears made from transport and work-oxen in the Kericho area has been confirmed at the laboratory. *T. vivax* is the usual parasite.

The original source of infection of these cattle is unknown; and it is impossible to account for the infection in the absence of the history of the oxen. There is no authentic evidence of the existence of a tsetse-belt anywhere near Kericho and one can only assume that the infected animals have, at one time or another, passed through a fly-belt. They may have been used for transport to and from Lolgorien; or they may have been purchased from the South Kavirondo Reserve where, in the Kuja river basin, tsetse-flies are abundant. *T. vivax* (and sometimes *T. congolense*) may be present in a beast without causing serious illness and death. A beast might tolerate trypanosomes in its blood for many months or even years. If such an animal contracts another disease—for example, rinderpest—or if it suffers from poverty (during drought) and is worked hard for a long period, it may " break down " to the disease and show numerous trypanosomes in a blood smear. In such cases trypanosomiasis is not the primary cause of death, but a blood-smear examination will reveal trypanosomes only.

Connected with this problem is the interesting record of a tsetse-belt in and around Kericho township, as shown on a map compiled by Lieut. A. F. Clarke, " I " Department, King's African Rifles, in 1921. It is difficult to explain this record, for no information is available as to what species of tsetse has ever been reported from that area. Perhaps the " belt " was inserted on account of the diagnosis of trypanosomiasis and the identification of trypanosomes in horses and cattle *at* Kericho. The animals might have arrived at the township to rest after having travelled through some of the tsetse-belts between Kericho and the Kenya-Tanganyika border, and they may have succumbed to the disease while at Kericho.

The difficulty of explaining these points, in connection with animal trypanosomiasis away from known fly-belts, indicates the need for accurate information on the distribution of tsetses which may serve for demarcating safe routes for movements of stock in time of peace as well as in time of war.

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AN ERIOPHYID MITE INJURIOUS TO TOMATO.

By A. M. Massee,

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Phyllocoptes lycopersici, Massee, sp. n.

Tryon, Rept. Queensland Agric. Dept. 1916–17, pp. 49–63. (No description.)

Body spindle-shaped, stout, tapering sharply towards anal end. Thoracic shield triangular, sides sinuate, apex produced and rounded, not completely covering rostrum. Centre of shield smooth, sides ornamented with two longitudinal furrows at end near lateral margins. Shield 44 μ long.

Thoracic bristles situated at posterior margin of thoracic shield, widely separated, mid-way between centre and lateral margins. Bristles stout, directed backwards, 14 μ long. Warts of thoracic bristles not conspicuous.

Rostrum short, curved.

Legs short, frail. First pair 34 μ long ; fourth joint 7 μ long, fifth joint 4 μ long. Second pair 30 μ long ; fourth joint 6 μ long, fifth joint 4 μ long. Feathered claw 3-rayed, conspicuous, 6 μ long. Claw of first pair of legs 6 μ long, stout ; second pair 7 μ long. Sternal ledge simple, short. The first pair of coxal bristles situated before anterior end of sternal ledge, and some distance from it. Second pair short and placed in line with centre of sternal ledge. The third pair just below posterior end of sternal ledge, in centre of inner coxal angle, 30 μ long, tapering towards apex.

Abdomen with smooth tergites, 27 in number. The ventrites are very numerous, very narrow, fine and smooth ; strongly punctated. Lateral bristles 20 μ long situated in line with epigynium. First pair of ventral bristles very long and conspicuous, 64 μ long ; second pair short, 12 μ long ; and third pair 20 μ long ; stout, tapering, hair-like at apex. Caudal bristles 74 μ long, fine. Accessory bristles absent. Epigynium pouch-shaped, 24 μ broad. Cover-flap smooth. Genital bristles directed downwards, towards anal lobe, 30 μ long. ♀ 200 μ long, 40 μ broad ; ♂ not known.

Host-plant : *Solanum lycopersicum*, L. (Tomato.)

Causes silvering and curling of the lower leaves ; the stem and leaf-stalks turn brown and the lower leaves and flowers fall off, and the fruits become stunted and rough-skinned. " Tomato rosette disease and fruit sterility " (Tyron).

Distribution : Stanthorpe and Bowen districts, Queensland, Australia (*Tryon*); Auckland, New Zealand (*W. Cottier*).

Described from spirit material collected by Mr. W. Cottier, M.Sc., Assistant Entomologist, Plant Diseases Division, Auckland, New Zealand ; received through the courtesy of the Imperial Institute of Entomology. Type vial in E.M.R.S. collection.

THE MOSQUITOS OF THE ISLAND OF CORFU, GREECE.

By Dr. Theodore Stephanides.

The following mosquitos have been observed by myself in the Island of Corfu in the course of a five year study during which more than 350 bodies of water, ranging from pools to small lakes, were examined.

1. **Anopheles maculipennis,** Meigen.

The larvae are found in the low-lying districts of the Island in shallow pools and irrigation ditches containing a medium amount of aquatic vegetation yet well exposed to sunlight. They are sometimes present along the edges and in the backwaters of drainage canals with an appreciable current, and frequently in slightly brackish (up to 10 per cent. salinity) waters by the sea-shore. They are most plentiful in Lake Antiniotissa among the floating masses of *Monostroma* (? *bullosum*, Roth-Wittr.) at the mouths of several fresh-water springs which flow into that shallow and slightly brackish mere from the south.

The adult bites most frequently after sunset and is the principal transmitter of the malarial parasite in the Island.

2. **Anopheles bifurcatus,** Linnaeus.

This is the commonest Corfu *Anopheles*. The larvae are present throughout the year, often in considerable numbers, in cool, shady ditches, springs and rills with a slight current and plenty of aquatic vegetation.

Though plentiful, *A. bifurcatus* is not of much epidemiological importance, so far as the climate of Greece is concerned, as the adults appear too late in the year to constitute a serious menace.

3. **Anopheles (Mysomyia) superpictus,** Grassi.

The larvae are met with, sometimes in great abundance, in small pools in the stony and pebbly beds of mountain rills where the water is warm and unshaded. In some of its habitats very little macroscopic aquatic vegetation was present, in others there were masses of *Cladophora* sp., but only on the bottom, leaving a layer of clear water on the top.

A tiny mountain spring near the village of Kouloura was particularly instructive as to the bionomics of both *A. superpictus* and *A. bifurcatus*. This spring formed two small pools, heavily shaded by bushes, which until last year contained great numbers of larvae of *A. bifurcatus* and only an occasional *A. superpictus*. Last summer the bushes had been cut by peasants for fire wood, and the pools now received the full force of the sun. This time I found them swarming with *A. superpictus* larvae, not one of *A. bifurcatus* being present. In view of the relative inocuousness of *A. bifurcatus* it is feasible that the presence of brushwood along mountain streams may sometimes be of importance in malaria prevention.

The adult seems to bite more freely during the day than *A. maculipennis*.

4. **Culex pipiens,** Linnaeus.

The commonest Corfu mosquito. The larvae are found in all bodies of water of not too great a size. They thrive both in open and in weedy pools, in the purest and in the most contaminated water. I have even discovered them in the oily and almost ink-coloured rain-water collected in disused olive-oil barrels. Their favourite habitat however seems to be shallow ditches with a mud bottom and little vegetation. The Corfu larvae resemble those described by Capt. Barraud from Mesopotamia, as they generally have a very long siphonal index (5 to 6·5) and 15 to 17 pecten teeth.

The adult is the mosquito most often met with in human habitations; it bites more freely by night.

5. **Culex laticinctus,** Edwards.

Much rarer than *C. pipiens*, but the larvae sometimes occur in swarms in ornamental basins, troughs and pools with clear water.

6. **Culex univittatus,** Theobald (*perexiguus*, Theobald).

Comparatively rare. The larvae, however, may sometimes be met with in fair numbers during the early summer among the aquatic vegetation along the margins of the larger ponds.

7. **Culex tipuliformis,** Theobald.

Apparently very rare, as I have only once (17.xii.35) observed a few larvae in a shallow weedy pool.

8. **Culex (Neoculex) apicalis,** Adams.

A common Corfu species. The larvae are found throughout the year in pools and ditches, especially those with copious aquatic vegetation. Sometimes in very slightly brackish (about 1 per cent.) water.

9. **Culex (N.) hortensis,** Ficalbi.

Found in the same habitats as the above but less plentiful. The adult can only be distinguished from that of *C. apicalis* after careful examination, but the larvae can be separated at the first glance. Those of *C. hortensis* have very long siphonal tufts (3 to 5 times the diameter of the siphon), whilst the tufts of *C. apicalis* are never longer than the siphonal diameter and sometimes completely lacking.

10. **Culex (Barraudius) modestus,** Ficalbi.

Very rare. So far I have only found (16.viii.34) two larvae in a water-butt among swarms of larvae of *C. pipiens*.

11. **Theobaldia annulata,** Schrank.

Very common. Larvae usually in shallow but fairly clear ditches, occasionally in wells. Gregarious with *T. longeareolata* and *C. pipiens* throughout the year.

The adult does not often enter habitations but bites freely in the open, both in the day and at dusk.

12. **Theobaldia longeareolata,** Macquart.

One of the commonest Corfu mosquitos. The larvae are observed throughout the year often in swarms, in shallow but clear ditches; also in water-butts, tanks and wells. They are extremely voracious and will attack the larvae of other mosquitos and even their own kind. The 3rd stage larvae are apparently the most predacious and will kill 4th stage larvae much larger than themselves. The nymphs are both light and dark coloured, the latter being slightly the smaller. The light-coloured nymphs produce female mosquitos and the dark males.

The adult is the largest Corfu mosquito, attaining a length of 8 mm. Its habits are the same as those of *T. annulata*.

13. Aëdes (Stegomyia) fasciatus, Fabricius.

Extremely plentiful. The larvae are found in all except very foul waters. They are often abundant inside houses in water-tanks, cisterns and even in flower-vases that may have been overlooked for a few days.

The adult is, with *C. pipiens*, the mosquito most often met with in habitations. It bites more frequently during the day and can be recognised, even before being seen, by its peculiar high-pitched piping.

14. Aëdes (Finlaya) geniculatus, Olivier.

Very rare. Two larvae only discovered (17.iii.35 and 24.xi.35) in a rain-water-filled hole in the trunk of an elm tree.

15. Aëdes (F.) echinus, Edwards.

Fairly common. I have often found the larvae in holes in elm and olive trees containing rain-water.

16. Aëdes (Ochlerotatus) zammittii, Theobald.

Common on the sea-coast where the shores are rocky, as the larvae are found in rock-pools containing sea-water. This water is often so salt from evaporation that brine-crystals have begun to be deposited and, in most cases, contains no other forms of animal life except a tiny Coleopterous beetle, *Ochthebius* sp.

The adult does not often enter habitations, but it bites freely on the sea-shore both in daylight and at dusk.

17. Aëdes (O.) detritus, Haliday.

Extremely abundant. Their larvae are met with in countless swarms (autumn, winter, spring) in pools, ditches and swamps of slightly brackish (2 to 4 per cent.) water by the sea-shore. Occasionally in quite fresh water with *C. pipiens* larvae.

The adults are not often found in habitations, nor do they seem to be very troublesome—taking their huge numbers into consideration—in the open.

18. Uranotaenia unguiculata, Edwards.

A rare mosquito whose larvae I have only found during the summer months, in a shallow and weedy ditch kept always full by water dripping from a moist clay bank.

Mosquito larvae are exceedingly scarce (so far as Corfu is concerned) in large, open, deep and permanent bodies of water. They are plentiful on the other hand in small and temporary collections or on the margins of large but shallow bodies of water and, for some species, in bays and pools along the course of slow-running streams.

The principal reason for this state of affairs is that mosquito larvae, with their short life-cycle, can develop in temporary bodies of water which are uninhabitable to their chief enemies, the larvae of the Coleoptera and Odonata, whose life-cycle requires as much as five years in some species.

Consequently the greatest prudence and circumspection should be exercised when draining bodies of water or treating them with larvicidal substances fatal also to the above-mentioned insect larvae. For, should the large bodies of water alone be attended to and the smaller ones overlooked or neglected, there is grave danger of destroying the breeding-grounds of the mosquitos' enemies rather than those of the mosquitos themselves and thus intensifying instead of abating the mosquito menace.

ON THE SYNONYMY AND BIOLOGY OF THE STRAWBERRY APHIS, *CAPITOPHORUS FRAGARIAE*, THEO. (1912).

By W. E. H. Hodson,
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(Plates X–XI.) C. pot

Introduction.

The high incidence of pathological symptoms in cultivated strawberry plants throughout the world has focussed the attention of numerous workers upon a study of the pests and diseases of the plants. In particular it has been shown in America, and more recently in England, that "virus" diseases are in part responsible for the present unsatisfactory state of the crops and that aphides are the vectors of at least some of these diseases. In England, recently, it has been shown that the virus disease, "yellow edge," which resembles or is perhaps identical with forms of virus infection prevalent in America and on the Continent, is freely transmitted by the aphis *Capitophorus fragariae*. Further, it has been suggested that such virus infections are a major trouble in the majority of the varieties of strawberry in cultivation at the present time. While this may or may not be the case, it is clearly of importance to study in detail the proven vectors of such diseases.

The present writer has considered the literature upon strawberry aphides and has for the past five years had the common English aphis under observation. This study has indicated that the actual synonymy of the insect is by no means accurately determined and that its detailed biology is not well understood. It is proposed, therefore, to consider the synonymy, to describe the various stages in the life-cycle and to contribute such notes on the biology, studied in field and laboratory, as are available.

Historical.

There is considerable literature upon species of *Capitophorus* infesting strawberries, but for the present purpose it will be sufficient to refer only to certain of the publications.

In 1901 Cockerell[2] described an aphis on strawberry in Arizona. The winged female and an apterous female (presumably from the leg measurements a viviparous form) only were described and were named *Myzus fragaefolii*. In 1912, Theobald[8] described from England similar forms of an aphis, which he named *Myzus fragariae*. Later Theobald[9] amplified this description under the name of *Capitophorus fragariae*. In 1914, Davidson[4] described from California winged sexual forms and eggs which he attributed to Cockerell's *M. fragaefolii*, but (apart from noting their presence) made no reference to the asexual forms. In 1931, Hottes and Frison[7] from Illinois discussed the synonymy of the aphis and stated that "*Myzus fragariae*, Theobald, is placed in the synonymy of *fragaefolii* because of determinations of Theobald, who named certain of our slide mounts from *Potentilla* as *fragaefolii*." They further referred to mating sexual forms taken by themselves, and in absence of evidence to the contrary it must be assumed that these tallied with those already described by Davidson.[4] Finally, in 1934, Harmsen,[5] from Holland, gave an account of sexual females which he attributed to the same species. He did not observe males, and his description of the females is merely a copy of that by Davidson.

(fragariae. These specimens seem to us to be identical with)
specimens of

The present writer in studying the aphis as commonly present upon strawberry in England has obtained in individual colonies four adult forms, namely, apterous and alate viviparous females, apterous oviparous females and apterous males. The latter at least have not been previously described. That the aphis is the species described by Theobald is tolerably certain, and in order that further confusion may be avoided it is proposed to redescribe, with measurements, the viviparous forms and to describe the sexual forms.

Description of Adult Forms.

Alate viviparous female (Plate xi, fig. *c*).

Head and antennae dark brown to black. Antennae longer than the body. Eyes dark red. Pronotum pale posteriorly, mesonotum with dark brown median area. Abdomen pale yellowish green, large dusky patch on apical half, dusky spots laterally and on basal segments. Wings with veins and stigma smoky black. Hairs capitate, generally distributed but abundant only at apex of abdomen ; four on front of head and a few variable ones on basal regions of antennae. Cornicles pale, faintly imbricated, not projecting beyond cauda, which is pale green, elongate, and has two pairs of lateral non-capitate hairs and one median subapical one. Legs pale, apical third of femora, apices of tibiae and tarsi dusky. Tip of rostrum dusky. Sensoria on antennae abundant, from 22 to 34 on seg. iii, average 28 ; from 4 to 10 on seg. iv, average 7 ; average total 35.

Average dimensions :—Length 1·20 mm., cauda 0·10 mm., cornicle 0·27 mm., hind femur 0·40 mm., hind tibia 0·84 mm. Antennae : segment 1, 0·07 mm., II, 0·06 mm., iii, 0·41 mm., iv, 0·25 mm., v, 0·24 mm., vi, 0·60 mm., total, 1·60 mm.

Apterous viviparous female (Plate x, fig. *c*).

Very pale green, sometimes almost translucent, becoming pale yellowish when old. Eyes red. Head, thorax, and body with many prominent capitate hairs. Basal portions of antennae, femora and tibae with few capitate hairs. Antennae pale, as long as body, sometimes extending just beyond the tips of cornicles. Cornicles faintly imbricated, pale and elongate, broader at base. Cauda pale, tapering with hairs as in alatae. Legs pale, almost transparent, tarsi and tip of rostrum dusky.

Average dimensions :—Length 1·33 mm., cauda 0·10 mm., cornicle 0·33 mm., hind femur 0·37 mm., hind tibia 0·71 mm. Antennal segments : i, 0·07 mm., ii, 0·06 mm., iii, 0·31 mm., iv, 0·23 mm., v, 0·21 mm., vi, 0·53 mm., total, 1·43 mm.

Apterous oviparous female (Plate xi, fig. *a*).

Lemon-yellow to pale orange. Eyes dark red. Head, thorax and body with many prominent capitate hairs. Basal portions of antennae. femora and tibiae, with few capitate hairs. Antennae pale, shorter than body, extending about to base of cornicles. Cornicles pale elongate, slightly curved inwards and expanded at base. Cauda pale, greenish yellow, tapering, with hairs as in alatae. Legs pale, hind tibiae a shade darker, tarsi and tip of rostrum dusky. Hind tibiae stout, with about 50 scattered sensoria.

Average dimensions :—Length 1·38 mm., cauda 0·10 mm., cornicle 0·27 mm., hind femur 0·30 mm., hind tibia 0·57 mm. Antennal segments : i, 0·06 mm., ii, 0·05 mm., iii, 0·19 mm., iv, 0·16 mm., v, 0·17 mm., vi, 0·49 mm., total, 1·13 mm.

Apterous male (Plate xi, fig. *b*).

Head dusky brown, eyes dark red to black. Thorax and body pale yellowish green. Mesonotum and abdominal segments with irregular dusky bands. Head, body and thorax with prominent capitate hairs. Antennae dark, base of segment iii paler, longer than body. Legs yellowish, apices of femora, bases and apices of tibiae, and the tarsi dusky. Cornicles, cauda and tip of rostrum dusky brown. Hairs on cauda as in previous forms. Cornicles short, expanded at base and nearly straight.

Sensoria on antennae abundant: from 8 to 12 on segment iii, average 10; from 4 to 8 on segment iv, average 6; from 3 to 6 on segment v, average 4; average total 21.

Average dimensions :—Length 0·91 mm., cauda 0·06 mm., cornicle 0·19 mm., hind femur 0·30 mm., hind tibia 0·61 mm. Antennal segments: I, 0·06 mm., ii, 0·05 mm., iii, 0·33 mm., iv, 0·19 mm., v, 0·18 mm., vi, 0·41 mm., total, 1·22 mm.

Egg (Plate x, fig. *a*).

Pale when laid, becoming black, shining. Length 0·55 mm., breadth 0·22 mm.

In the foregoing description of the adult forms, the single subapical sensorium on segment v and the group at the apex of the basal area of vi of the antennae have not been included in the totals given, as they are constant in all forms.

Discussion.

The above description is the first made of the four adult stages of the aphis as occurring in individual colonies, and on examination it is found that certain earlier descriptions do not appear to apply to the same insect.

The description by Cockerell[2] of viviparous forms is less complete than could be desired but differs slightly from that of the present species in that in his *fragaefolii* antennal segment iv is shorter than v in the apterous viviparous female. In the insect under present consideration this is never the case, whilst the cornicles are relatively shorter and the hind tibiae longer than those of Cockerell's specimens. Also the distribution of capitate hairs upon head and antennae is not in the present species an entirely constant character. The original description of the alate form is not sufficiently complete to justify specific determination.

The writer has examined a slide mount labelled *fragaefolii*, in the British Museum of Natural History, which was received from Cockerell at about the time that he described his species. It is probably part of the original material, and whilst the aphides have a marked resemblance to the species now under consideration, the state of preservation is such that critical comparison is not possible.

Sexual forms as described by Davidson[4] are very markedly different. In the present species the oviparous female has no dusky covering to the head, the cornicles are not curved at the apex, the cauda is not dusky, there is not a prominent group of non-capitate hairs beneath, and the relative measurements differ. The male is apterous and quite dissimilar. Further to this point Hottes and Frison[7] in discussing the synonymy, and it was principally on their discussion that the present insect came to be included as *fragaefolii*, refer to mating sexual forms which presumably, as they make no note to the contrary, conformed with those described by Davidson.[4]

Reverting to a consideration of the viviparous forms, Balachowsky[1] states that material from France was identified by Frison as being identical with American forms, and that material sent to him from Illinois was apparently identical with Theobald's *fragariae*. Also Laing (*in litt.*) informs the writer that Dr. Preston W. Mason, U.S. Bur. Ent. Washington, has seen English specimens and considered them *fragaefolii*.

Certainly these viviparous forms conform very closely with those described by Theobald.[9] Relative proportions are similar, and there is every justification for assuming that they are one and the same species. At the same time they are almost indistinguishable from viviparous forms from America, although, as pointed out previously, actual relative dimensions of English specimens differ somewhat from those recorded in the original description by Cockerell.[2]

In the case of the sexual forms the differences are much greater, for even if it be assumed that both alate and apterous males may occur in the one species, a phenomenon not unknown, there are other marked differences, *e.g.*, in the distribution of sensoria on the antennae. Further, the oviparous females are markedly dissimilar.

In the present instance asexual forms are described from specimens collected in various localities, checked by individuals bred under controlled conditions. Sexual forms are described from many individuals arising both in 1935 and 1936 in several colonies established on pot-plants. These colonies originated in each instance from individual viviparous aphides. Thus, the possibility of more than one species being included in the description is entirely eliminated.

It is freely admitted that further knowledge may show that there is but one very widely distributed and variable species to consider, viz., *Capitophorous fragaefolii*, Cockerell. Nevertheless, it is more than likely that there are in fact more than one closely allied species which, whilst almost indistinguishable in the viviparous forms, have clearly differentiated sexuales. This phenomenon is well known among aphides, *e.g.*, *Aphis helichrysi*, Kalt., and *A. marutae*, Oestl., are said to be indistinguishable in the viviparous forms, but *helichrysi* has an alate and *marutae* an apterous male, and the oviparous females are said to differ slightly. Also in *Aphis pomi*, DeG., and *A. spiraecola*, Patch, similar conditions are said to occur.

From the foregoing it is concluded that the common strawberry aphis in England is that described by Theobald[8] namely, *Capitophorus fragariae*, and that although very similar to it it is not identical with the American form *C. fragaefolii* Ckll.[2] and certainly not with the sexual forms attributed to *C. fragaefolii* by Davidson.[4]

Biology in the Field.

In England apterous viviparous females are, throughout the year, present on the undersides of the leaves of strawberry plants, usually sheltering at a junction of midrib and vein. Their presence in winter in similar situations has been observed in Holland by Harmsen,[5] who records their occurrence outdoors at a temperature of −10°C. On the other hand, Balachowsky[1] has doubted the ability of the aphis to overwinter outdoors in Central France, unless sexuales lay eggs in October which overwinter. He, however, produces no evidence in support of this suggestion and has not observed sexuales of this or an allied species of aphid.

Over a number of winters the writer has observed that in southern England asexual reproduction continues in mild spells during every winter month. Low temperatures, even when persisting for considerable periods, cause no mortality to adults or nymphs. On the other hand, periods of wet weather, particularly when rain is heavy and continuous, whereby the undersides of leaves become splashed with soil and grit, may destroy up to 70 per cent. of individuals present in the open field.

The aphis is apparently ubiquitous in commercial strawberry-growing areas in England, but the actual size of the winter population varies from plant to plant and field to field. Quite commonly some 5 to 20 individuals, in various stages of growth, may be found upon a single plant, representing an overwintering population of the order of 150,000 to 500,000 aphides per acre of plants.

In March the rate of reproduction increases, and by late May or early June populations often reach epidemic proportions.

Mature alate females have not been found outdoors before early June, but nymphs of this form have sometimes been seen in January, this indicating that the adults probably occur sparingly in early spring. From June onwards alatae are present, often in quantities, until late into the autumn. They are active and restless, in favourable weather leaving the plants freely, and have on occasion been observed upon the wing in swarms in the vicinity of heavily infested plantations.

From late June until September the total aphis population usually tends to fall materially. In hot dry weather the rate of reproduction diminishes, rising sharply again in September, when large colonies are once more built up.

Sexual forms have not been found in the field, despite intensive search. This may be explainable on the score that they are not, as observed under experimental conditions, ever very numerous and so easily escape notice. Nevertheless, ova, which have appeared to be identical with known eggs of the species, have sometimes been found in heavily infested plantations.

Host-plants.

It has been suggested that the comparative scarcity of the aphides upon strawberry at some seasons of the year might be traceable to their migration to alternative host-plants. Whilst this possibility cannot be entirely discounted, no evidence that it is really the case has been obtainable.

Frequent examinations in the vicinity of infested strawberry fields have never disclosed the presence of the aphides upon plants other than strawberry. Also alate females, taken on the wing or removed from plants, have readily settled upon and remained and reproduced upon strawberry plants. Further, as will be shown, sexual forms occur upon the strawberry.

In the field the writer has only found the aphis on cultivated strawberry, but has induced it to colonize freely upon wild strawberry, potentilla, and cultivated rose. On all these hosts it has lived asexually for several generations without any apparent loss of vigour, and has then readily returned to cultivated strawberry.

In England Davidson[3] gives strawberry and *Centhranthus ruber* as hosts, but the writer has been quite unable to induce the aphis to live upon the latter plant. In America the known hosts of the allied form or species are, according to Hottes and Frison[7] *Rosa rugosa*, *Rosa* sp., *Potentilla monspeliensis*, *Potentilla* sp., and *Fragaria* sp.

In the opinion of the writer it seems that the inclusion in the annual cycle of a host-plant other than strawberry is unnecessary. Colonies have been maintained continuously upon strawberry for over two years without exhibiting any sign of etiolation. The rate of reproduction has remained entirely comparable with that obtaining in young colonies originating from individuals collected at intervals in the field. Further, there has been no reduction in fertility or in size of individuals after at least 20 consecutive viviparous generations upon the plant.

Biology in the Laboratory.

It is well known that when strawberry plants are placed under glass, *e.g.*, for forcing out of season, populations of this aphis are likely to rise rapidly to epidemic proportions. Under laboratory conditions the same holds good, and only to a very limited extent can observations made therein be considered applicable to behaviour in the field.

On pot-plants kept at ordinary laboratory temperatures (45°F. to 65°F.) the life from newly emerged nymph to adult may occupy from 13 to 25 days for apterous viviparae, a few days longer for alatae. Adult viviparous apterae have lived for from 15 to 25 days, perishing rapidly if deprived of food. Mature alatae have lived up to 14 days without food provided that atmospheric humidity has been suitable.

In Holland, Harmsen[5] having bred the aphis upon leaves in petri-dishes, has set out a general life-cycle in which alatae invariably gave rise to viviparous apterae which usually produced viviparae, both apterous and alate, plus oviparae, but never males. In fact, he never observed the latter form.

The writer, under less artificial conditions, in that the aphides were upon growing plants, has found no such well-defined cycle. Alatae have usually produced apterous viviparae but occasionally also a few alatae. Apterous viviparae arising from alatae have produced usually both apterous and alate ~~apterae~~ viviparae. Only in one generation in each year have sexuales been produced. These have always arisen from apterous viviparae which individually have produced sexuales in small numbers, viviparous apterae in larger numbers, but never alatae.

Considerable interest attaches to the fact that only in one generation each year have sexuales been produced, and invariably in December and January. The time of appearance has remained constant within this period, regardless of whether colonies have been in the laboratory for over 12 months previously or have been brought indoors as late as the November immediately preceding such occurrence. In recently brought-in colonies the sexuales have appeared during the first generation, except in one instance in which they must almost certainly have been present as nymphs outdoors. The indication is that the normal time of occurrence of sexuales outdoors is as late in the year as December.

These forms have never been observed in abundance, only some half-dozen or so arising in individual colonies consisting of very many individuals. In some colonies males and females have arisen in approximately equal numbers, whilst in others males or females only have been found. In some colonies sexuales have not appeared at all during as long a period as eighteen months.

Both alate and apterous viviparae are active during warm weather and even the latter migrate freely amongst adjacent plants. The alatae, as previously stated, may occur freely upon the wing on bright still days and can undoubtedly remain without food for comparatively long periods and travel considerable distances. In the laboratory when plants are exposed to sunshine the whole alate population tends to leave and congregate on the windows, but the apterae only move in quantity if the plant becomes seriously overcrowded.

As previously related, sexuales have not been found in the field and any account of behaviour can only relate to that under artificial conditions.

Males are very active, feed freely and wander over the leaves in search of oviparae. Their adult life has extended to 8–10 days. Oviparae are active before fertilization, becoming more sedentary later, and have lived for 13 to 18 days. Usually each contains 4, sometimes 5 eggs, which when developed occupy almost the whole of the body cavity.

Eggs have been deposited singly, sometimes on the undersides of leaves, sometimes upon stipules and around the base of the plant. Observed females invariably died without ovipositing when not fertilized. Egg mortality has been high, probably on account of abnormal temperatures and humidity in the laboratory. Some hatched in late February and early March produced viviparous apterae apparently identical with the common asexual form.

The process of hatching from the egg has been observed. First the egg loses its symmetry, becoming depressed. Then an end is ruptured and the aphis squirms its way out, head first. The complete process occupies some 15 minutes, and the newly emerged aphis immediately settles down and feeds for some hours before leaving the vicinity of the egg.

Pathological Aspects.

As noted at the commencement of this paper the aphis is a known vector of at least one virus disease of the strawberry. Apart therefore from the mechanical injury which it may cause, its presence is a serious matter in relation to the health of a plantation. The present study has sufficed to indicate that the aphis has no necessity to leave a plantation in search of an alternative host-plant, and in fact once established it will persist indefinitely and breed throughout the year.

Spread from any distance is by way of alatae and is confined to the warmer months, but apterae will slowly spread by way of adjacent plants until distributed over a wide area. There is some evidence that sexuales oviposit in late autumn, the eggs hatching in early spring. This means of survival and increase is perhaps not of great importance in England, where viviparous reproduction is practically continual. It may, however, afford the sole means of overwintering in colder climes.

Control Measures.

It has been accepted that aphis-free plantations can be established by the subjection of plants to hot water treatment, prior to planting.[6] In view of the fact that ova may be present, the effect of the treatment upon them must be examined. This is being done, although apparently they would not normally be present at planting time.

The problem of maintaining established plantations in an aphis-free condition is much more difficult. For nearly six months in the year plantations are exposed to possible infection by winged aphides from elsewhere, and unless the plants are grown far from likely sources of infestation, the aphis is certain to become established. In areas in which strawberries are grown commercially only rarely is a sufficient degree of isolation obtainable, and it would therefore appear that resort to routine applications of insecticides is unavoidable.

Unfortunately extensive trials, using both dry and wet insecticides, often at very frequent intervals, have failed to give a high measure of control. This lack of success has not been due to any quality of resistance in the aphides, but to failure, purely on mechanical grounds, to cover the plants effectively. The prostrate habit of the strawberry makes it virtually impossible to coat the undersides of all leaves with dust or liquid.

No very complete control of the aphis, under field conditions, is likely to be achieved until a considerable advance is made in the technique of the application of insecticides. In view of the serious results attending continued infestation, strenuous efforts should be made to solve this very urgent problem.

In conclusion, the writer wishes to express sincere thanks to Mr. Laing, of the British Museum of Natural History, for his sustained interest and very material assistance in the preparation of the first portion of this paper. Thanks are also due to Mr. Boyd, University of Reading, for help in field and laboratory.

Summary.

1. Reference is made to the proven capacity of aphides of the genus *Capitophorus* to transmit virus disease among strawberries, and attention is drawn to the confusion existing as to the actual synonymy of the insect principally concerned.

2. For the first time sexual and asexual forms of the species commonly present in England have been observed together. Evidence is considered which suggests that the aphis is *Capitophorus fragariae*, Theo., and that American forms are in reality other, but closely related, species.

3. The incidence of the aphis in the field is considered, and the biology as observed in field and laboratory is discussed.

4. The economic significance of the aphis is referred to, and attention is drawn to the practical difficulties attending efforts to keep it in control, particularly in commercial strawberry-growing areas.

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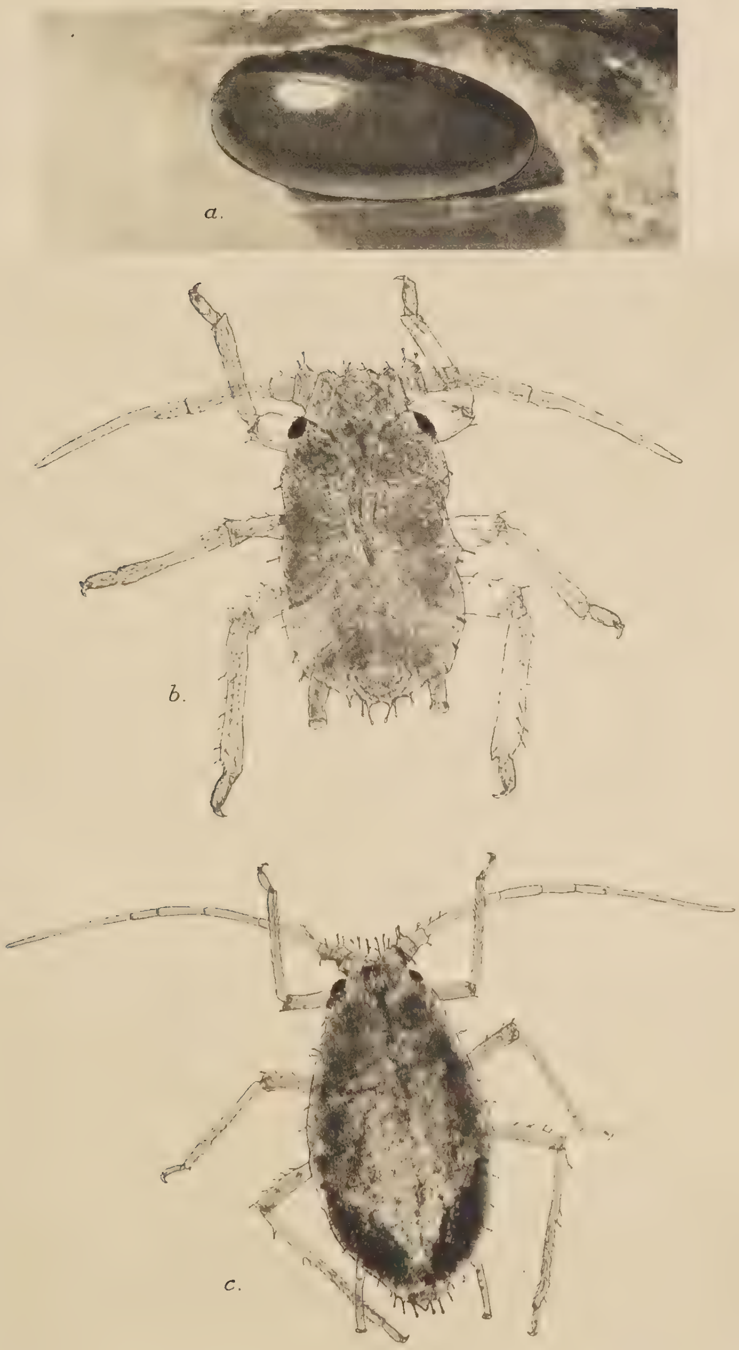

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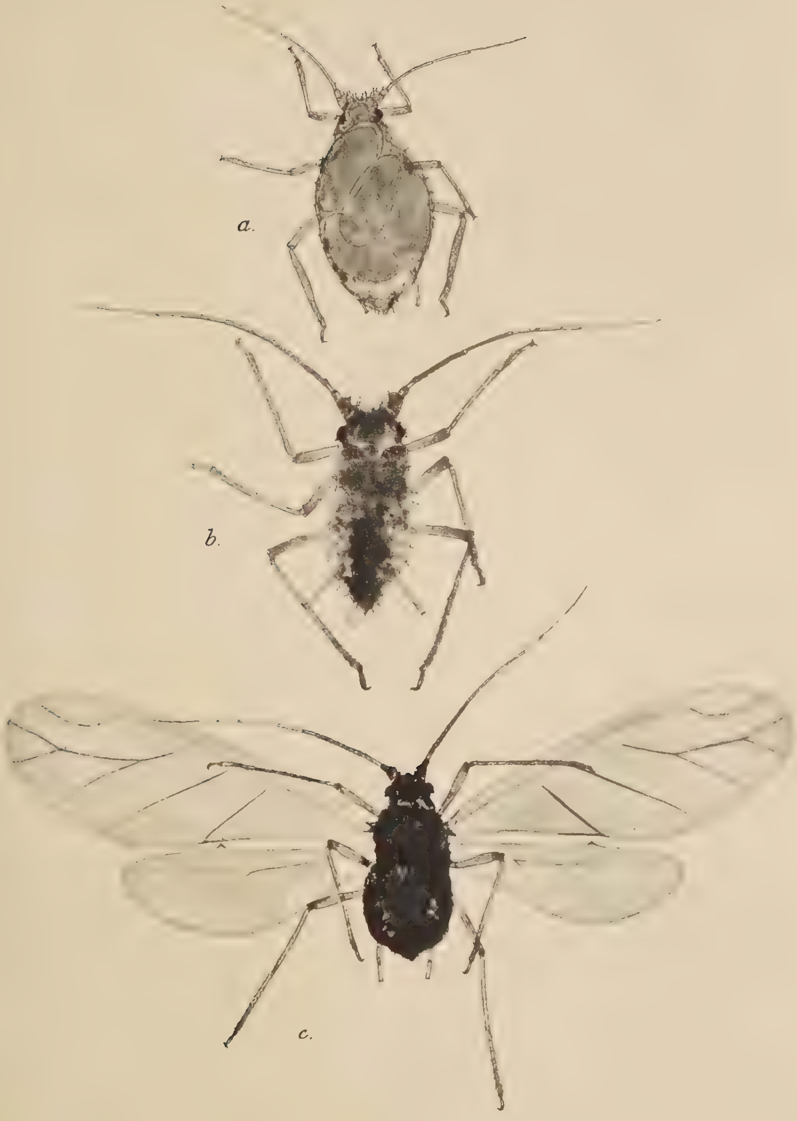
Capitophorus fragariae, Theo.: *a*, ovum (x82); *b*, nymph (x80); *c*, apterous viviparous ♀ (x38).



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Capitophorus fragariae, Theo.: *a*, oviparous ♀ (x22); *b*, ♂ (x22); *c*, alate viviparous ♀ (x32).

NOTES ON THE DEVELOPMENT OF RED LOCUST HOPPERS (*NOMADACRIS SEPTEMFASCIATA*, SERV.) UNDER NATURAL CLIMATIC CONDITIONS.

By C. Smee, M.C., D.I.C., F.R.E.S.

During the years 1933 to 1936, when the Nyasaland Protectorate was invaded by the red-winged locust, considerable variation in the rate of development of the hopper bands and the intensity of the resulting flying swarms in different parts of the country during the second year was a very noticeable characteristic (Smee, 1936). The phenomenon was even more marked during the 1934–35 and 1935–36 breeding seasons when hopper bands often failed to reach the adult stage, or the resulting adult swarms were of a much smaller size than was anticipated. At the same time, in the Shire River valley at the southern end of the Protectorate, development appeared to progress normally and on a large scale during all the four seasons.

It did not seem possible that destruction by parasites, fungus disease and human agency could be entirely responsible for the decrease in the development of new swarms, and the scattered and quiescent nature of the hopper bands in many places during 1933–34 and 1934–35 was obviously due to some other cause, presumably climatic conditions.

Preliminary Examination of Climatic Conditions.

Comparison of the temperature and humidity factors over the four years for five stations, three years for one station and two years for two other stations, where differing rates of hopper development and varying intensity of new swarm production had been observed, indicated that the year of initial invasion was generally rather hotter and drier than the succeeding years. It was also apparent that both the lower and upper Shire valleys experienced more consistent temperatures and humidities, during the hopper period, than the other areas where similar records were kept.

Climatographs of the mean monthly maximum temperature and the mean monthly percentage of relative humidity for the critical months of hopper development, December to March, were drawn, and it was seen that during these four years there was a tendency towards an increase in humidity and a decrease in temperature, and that the most successful breeding and development appeared to take place at temperatures above 85°F. and below 80 per cent. relative humidity.

Up to this point little, if any, data as to suitable or unsuitable conditions for hopper development of this locust were available. When the results of Dr. A. G. Hamilton's experiments on hopper development under controlled conditions of temperature and humidity came to hand (Hamilton, 1936), it became possible to review the conditions occurring in nature in more detail.

In the first place, it appeared of interest to compare the favourable conditions for hopper development (between 60 and 70 per cent. R.H. and above 90°F.) as given by that author with the field data. Secondly, it seemed desirable to do the same with regard to conditions of sexual maturation, by including the months of October and November in the study. It was, unfortunately, found impossible to obtain sufficiently reliable data from any satisfactory number of stations to warrant comparative consideration of the conditions occurring during the egg-stage. In many cases actual oviposition was not observed, and it would only have been possible to judge the date of egg-laying by the date of hopper emergence. Considerable destruction of egg-packets by Meloid larvae and other predators was known to have occurred in some areas in different years and therefore probably also in unrecorded places. Further, it seemed possible to the writer that other factors than atmospheric temperature and humidity might have influence on the egg incubation period and the number of resulting hoppers. The work was therefore confined to the period when sexual maturation might be expected to be taking place and that covering the actual existence of hopper bands.

Climatographs of Critical Months.

Climatographs, for as many stations as possible, were prepared for the months October to April inclusive with the suitable range of conditions for sexual maturation as shown by Hamilton (45–75 per cent. R.H. and 90°F.) superimposed on them, and the apparent limits for hopper development under natural conditions (80 per cent. R.H. and 85°F.) added also. These bioclimatographs (Uvarov, 1932) are given, in series for the various stations, as figures 1–9. For the location of the stations the reader is referred to the map published in an earlier paper (Smee, 1936).

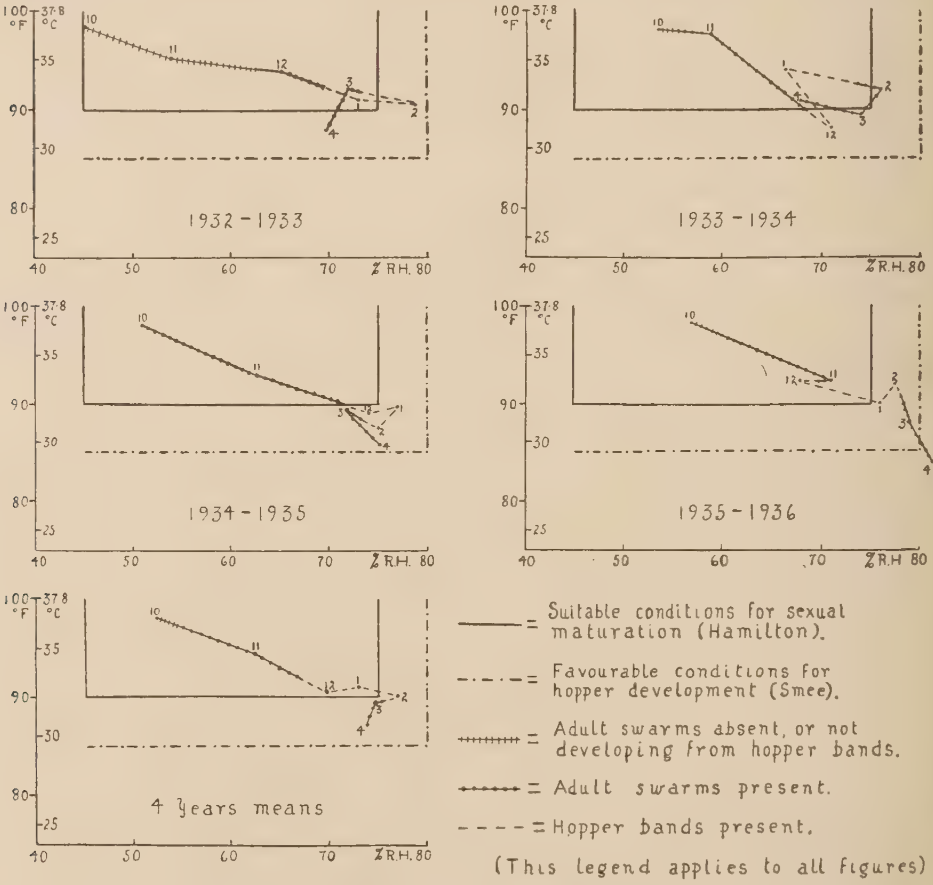

Fig. 1. Port Herald.

Fig. 1. *Port Herald* (115 feet).—This station is in the lower Shire River Valley, where the development of the locusts was practically normal in all four years, though

becoming slightly less intense during the last two seasons. The time taken by the hopper bands to become adult in each year was 67–68, 56–60, 65–70 and 70–75 days respectively. It can be seen at once that the conditions here approximate very closely to Hamilton's minimum temperature range, particularly so in the 1933–34 season, when the favourable humidity conditions of 60–70 per cent. were also experienced during December and January at the beginning of hopper development, and in this year the time of hopper development was the shortest recorded. In the first year hoppers did not occur until January, the mean relative humidity of which was only just above 70 per cent., and though February registered nearly 80 per cent., March humidity was again only just above 70 per cent. Hamilton (*l.c.* p. 55) states that " hoppers which have passed the first instar are more able to withstand extreme conditions of humidity and temperature than first-instar hoppers." In the three following seasons hoppers hatched first in December and it would appear that first-instar hoppers would have experienced, therefore, conditions not very far removed from the optimum.

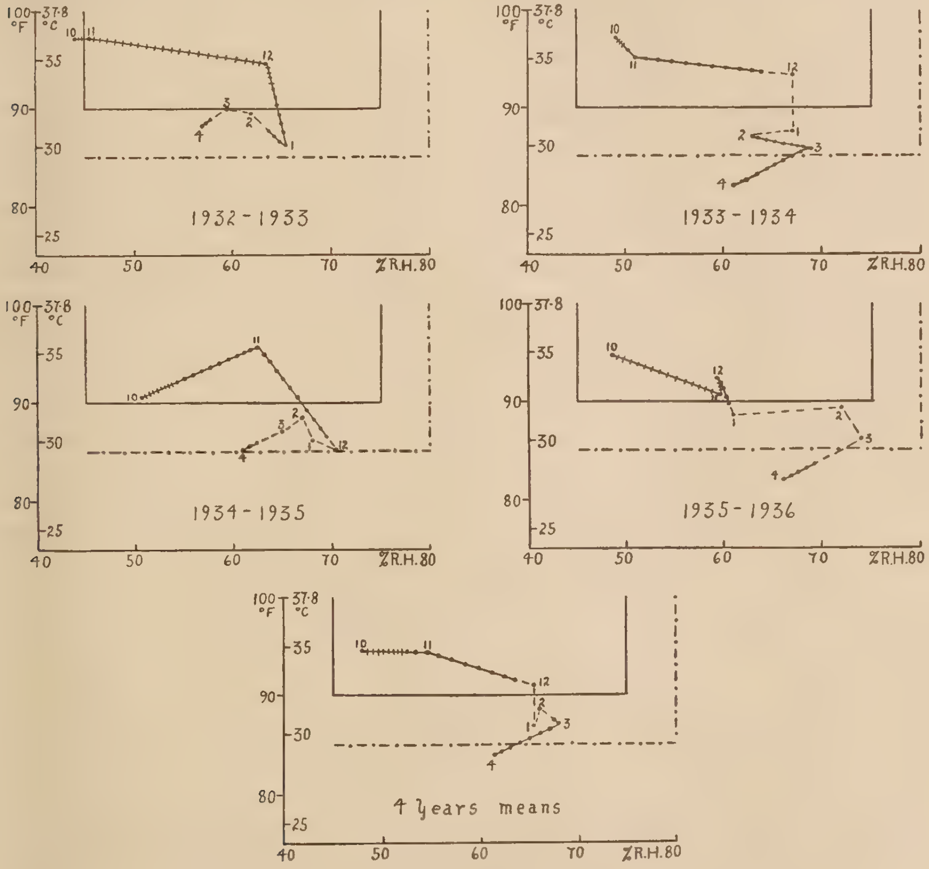

Fig. 2. Fort Johnston.

The climatograph of the four years' means for this station shows the critical months for hopper development to register a mean maximum temperature of just about 90°F. and a mean relative humidity of 70–77 per cent. Hamilton (*l.c.* p. 12, Table 3) obtained normal hopper development and a high percentage of adults at this temperature and at both 70 and 75 per cent. relative humidity.

Fig. 2. *Fort Johnston* (1,550 feet).—This station is situated at the south end of Lake Nyasa and would appear to have conditions generally suitable for normal development of hopper bands. During the first two seasons this did occur. In 1933, hoppers hatching in February became adult in 64–68 days, and in the following season hoppers in December and January became adult in 66–70 days. In both years it will be seen that these months are within or near the favourable conditions of both temperature and humidity for first-instar hoppers. During the 1934–35 season, however, only slight development of new swarms was recorded. Hoppers certainly appeared in December and January, when the maximum temperature was only 85°F., which may have placed the first-instar hoppers under unfavourable conditions.

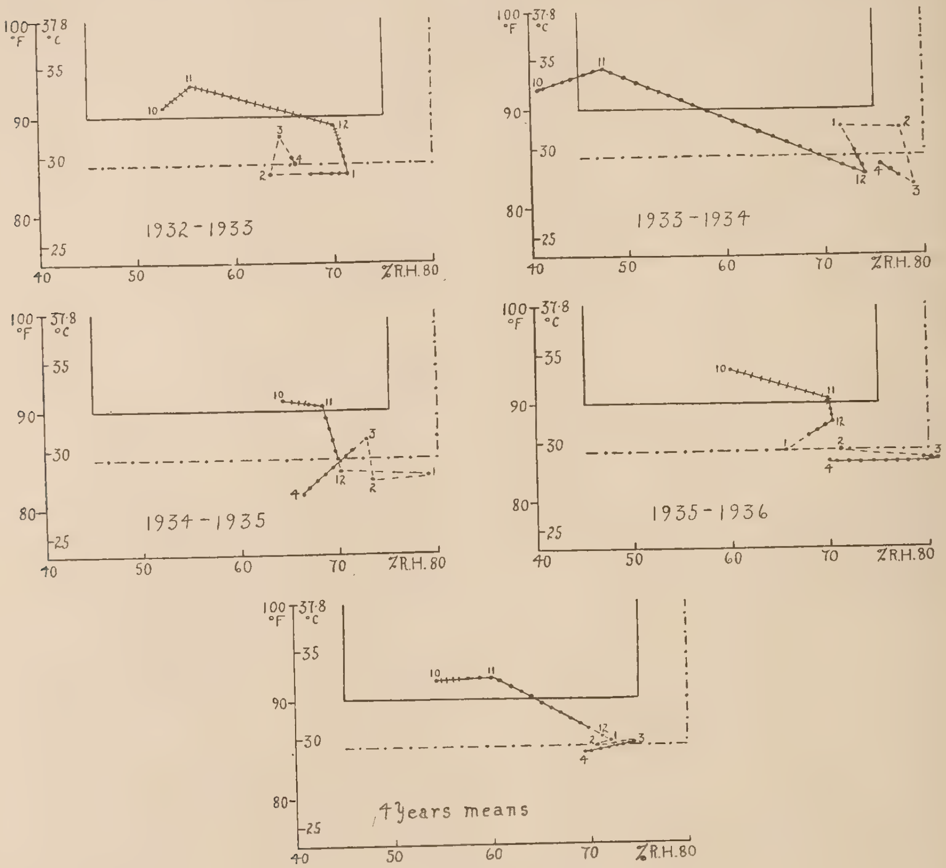

Fig. 3. Balaka-Liwonde.

The fungus disease, *Empusa grylli*, was certainly present early in the season, and owing to an exceptional rise in the lake level, areas which had been thickly laid over in the previous two years were inundated. Nevertheless the failure of swarms to develop on the anticipated scale is somewhat obscure, as the conditions in general would appear just as suitable as in other years and places. It is perhaps worthy of note, however, that though swarms re-invaded the area in November, the conditions during December were, *in this year only*, outside the limits of successful sexual maturation of the adults. In 1935 only one breeding swarm was recorded as arriving near the station on 30th December. Development from this one swarm occurred, the hoppers taking approximately 80 days to become adult.

The climatograph for the four years' means indicates that this station would be suitable for continual normal hopper development, but the fact remains that such has not been the case. From the available records it seems that a somewhat similar situation occurred here during the previous locust cycle; reports were made of considerable quantities of hopper bands, but after the initial generation or two the resulting adult swarms were few.

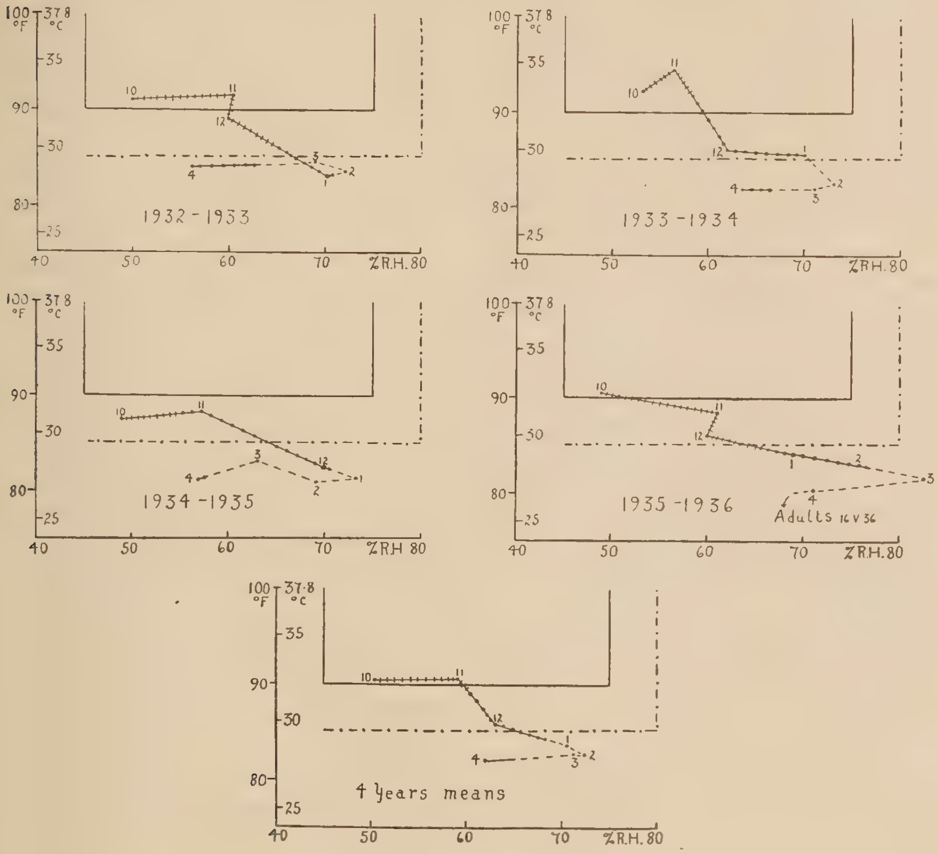

Fig. 4. Nkwale.

Fig. 3. *Balaka-Liwonde* (1,500 feet).—This area comprises the upper part of the Shire River Valley, and breeding occurred here in all four years in a very interesting variable manner. From the initial invasion in 1932 hoppers occurred in February 1933 and became adult in 63–68 days. Although the temperature appears to be low to begin with, it improves slightly in March and the humidity is within the favourable limits. In 1933–34, with a somewhat higher temperature (88°F.) and a relative humidity of 71–78 per cent., the development of hoppers hatching in January was considerably slower, requiring 80 days for them to become adult. In 1934–35 development was again slower, covering a period of 80–90 days for hoppers that hatched in December. Conditions for the first-instar hoppers would not seem to have been quite as suitable as previously. In the 1935–36

season hoppers appeared in January and February under slightly better conditions than in the previous two years and development was not so delayed, new swarms appearing in 70–75 days. The climatograph for the four years' means places this area just on the temperature limit of 85°F. that had originally been selected as the possible minimum for successful hopper development. The consistency of both the temperature and the humidity during the critical months is rather remarkable.

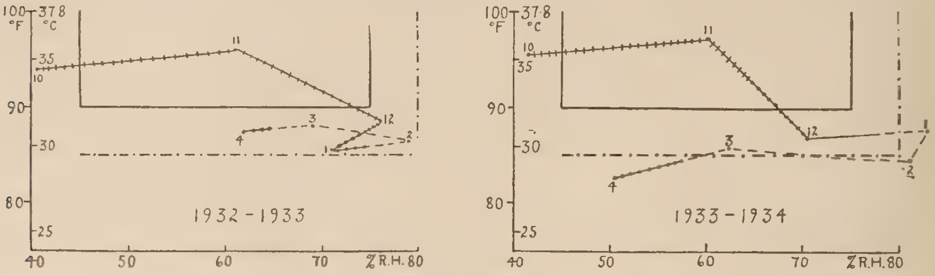

Fig. 5. Salima.

Fig. 4. *Nkwale* (1,800 feet).—This station lies some 20 miles westward from the lake shore at Domira Bay, towards the foothills. The results of breeding and development here are somewhat comparable with what occurred in the Balaka-Liwonde area, with a more pronounced delayed development in the third year. Hoppers from the initial invasion did not hatch until February, but developed normally in about 65 days. During this period the temperature was in the region of 85°F. and humidity generally in the vicinity of 70 per cent. In the following season hoppers again hatched in February and with a slightly lower temperature required 75 days at least to become adult, the quiescent and scattered nature of the bands being very marked. In 1934–35, although adult swarms arrived in November, hoppers did not appear until January. Development of new swarms was practically negligible and no accurate records of the time of development could be obtained, though a period of over 100 days seemed indicated. First-instar hoppers would seem to have experienced unsuitable conditions and the low temperatures from October to December may have influenced the sexual maturation of the adults. During the 1935–36 season breeding swarms did not arrive until late in January and were only a few in number. Oviposition was very light and development of hopper bands took some 77 days. Resulting adult swarms were small and there was considerable evidence of the phase *dissocians* habits. The climatograph for the four years' means indicates that this area has less suitable conditions for hopper development than the places previously discussed, and further, that the months when sexual maturation of the adults might be expected are of doubtful suitability.

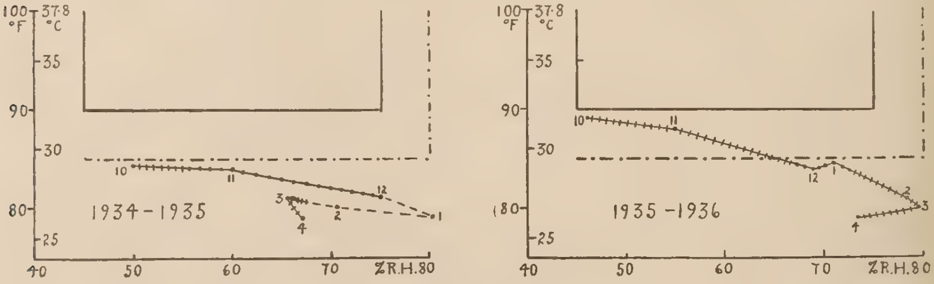

Fig. 6. Likuni.

Fig. 5. *Salima* (1,669 feet).—This station lies on the lake shore plain between Nkwale and the lake. Climatic records are available for the first two years only of the locust invasion, but these are of interest when compared with the same years at Nkwale. From the initial invasion, hoppers hatched in February and became adult in 64 days. In the second year the same, if not more, delayed development of 75–80 days was experienced as at Nkwale, but the resulting swarms were certainly more numerous and larger in size. In both years it will be seen that conditions in March improved considerably over those of February. During the next two seasons (climatic records not available) breeding and development became less intense, very similar to what occurred at Nkwale, but slightly greater in volume, probably owing to the temperature being somewhat higher.

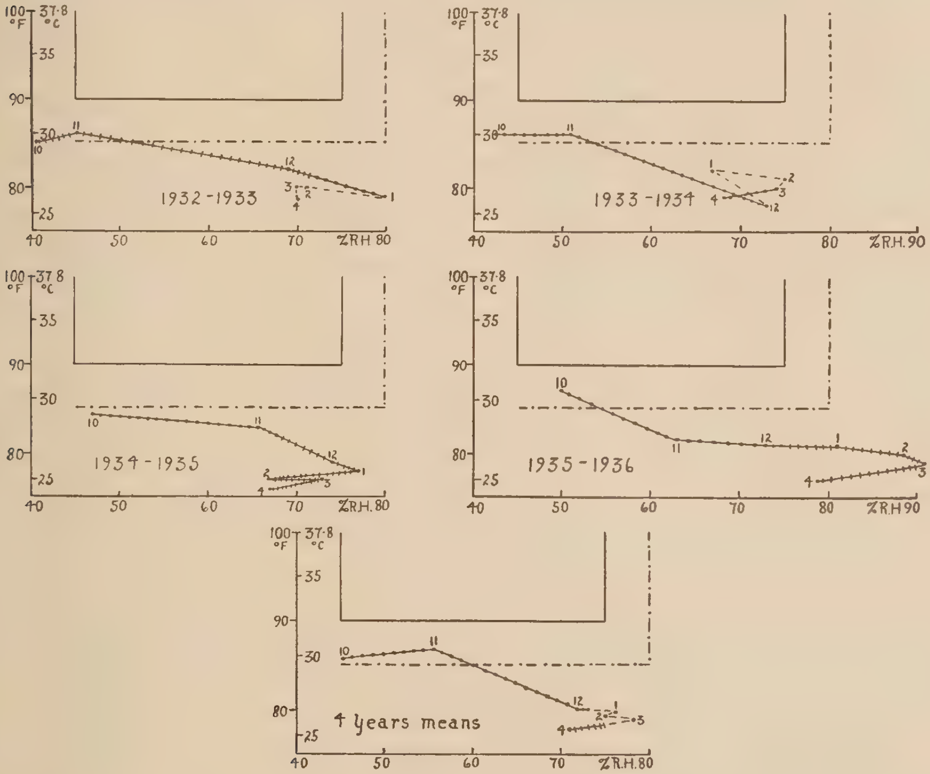

Fig. 7. Zomba

Fig. 6. *Likuni* (3,600 feet).—This station is situated in the Central Angoniland plateau. It was in the direct line of flight of the initial invasion swarms and during the first two seasons was heavily infested with hopper bands. Humidity records for these two seasons are, unfortunately, not available, but the development of hoppers in 1933 took 85 days when the mean maximum temperature during the critical months was in the vicinity of 80°F. In the 1933–34 season development was very considerably delayed, over 100 days being recorded, the maximum temperature being generally below 80°F. The climatographs for the 1934–35 and 1935–36 seasons indicate that conditions would not be suitable for hopper development. In the former year, though breeding swarms arrived in November and December and oviposited, and a few hopper bands were recorded in January and February in the vicinity, no complete development appeared to take place. In the latter year one swarm only traversed the area in January, but no oviposition occurred.

Fig. 7. *Zomba* (3,000 feet).—This station, situated on the south-eastern flank of Zomba mountain, was itself only infested with hoppers to a slight extent after the initial invasion in 1933. Hoppers hatching in February took some 80 days to become adult and the main development of swarms occurred more towards the plains than on the slopes of the mountain. Although adult swarms were circulating round Zomba during nearly the whole of 1933 up to November of that year, development in the 1933-34 season occurred only some distance away from the station. Hoppers hatched in January and February required 87–90 days to become adult and the resulting swarms were few. The climatographs show that in these two seasons the temperature during the critical period was in the region of 80°F. with a relative humidity of 70–75 per cent. Hamilton (*l.c.* p. 12, Table 3) records one experiment at 80°F. and 75 per cent. relative humidity when a small proportion of hoppers became adult. In the following two seasons, although adult swarms were present in the near vicinity in September and November 1934 and in November and December 1935, no breeding or oviposition took place in the area to which the meteorological records would refer. Development in the plains was also markedly delayed. The increase in humidity in 1935–36 over previous years was considerable. The climatograph for the four years' means shows the temperature from December to April to be well below the suggested minimum of 85°F. and the preceding two months to be outside the range of temperature and humidity suitable for sexual maturation.

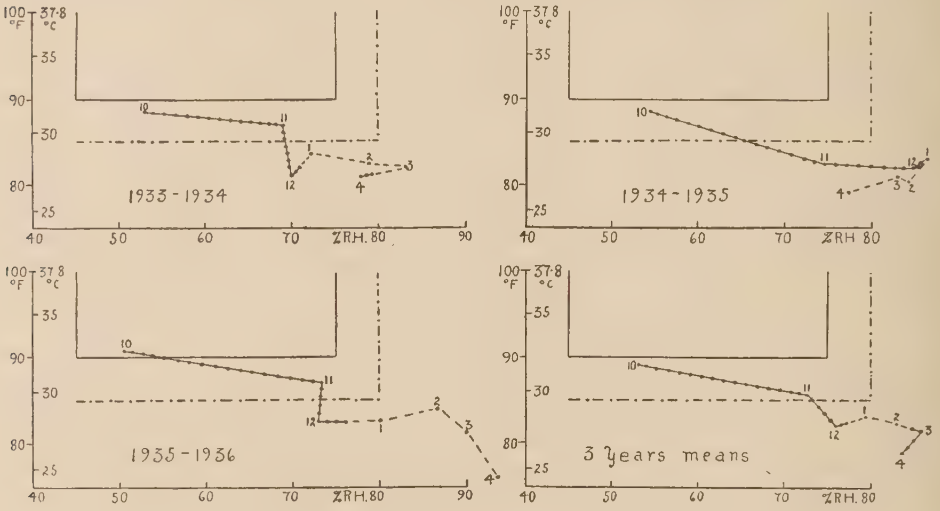

Fig. 8. Mlanje.

Fig. 8. *Mlanje Experimental Station* (2,300 feet).—The station where these records were taken lies on the south-east flank of the Mlanje massif in the tea-growing area where the annual precipitation is considerably greater than at other sides of the mountain. The initial invasion of this area by sexually immature flying swarms occurred in June 1933. Later in the year slight breeding and oviposition took place, and some hopper bands appeared in January, taking approximately 90 days to become adult, but, in general, development was negligible. During the whole of 1934 and 1935 swarms were passing through or circulating in this area, coming apparently mainly from the lower elevations of Portuguese East Africa to the south, yet no further breeding or development took place on this flank of the mountain. It will be seen that in these two latter years the humidity conditions diverge very

greatly from the apparently suitable range. The climatograph for the three years' means for this area shows that the months October to December are well outside the limits for sexual maturation and that the humidity during the critical months of hopper development is 80 per cent. and more.

Fig. 9. *Dedza* (5,250 feet).—This high area of the Angoniland Plateau was in the direct line of flight of the initial invasion in 1932–33. Apart from slight hopper development in much lower-lying valleys in the vicinity in this first season, no breeding or development has occurred here, although swarms have been recorded passing through the area from time to time each year, including those months when breeding might be expected. From the climatographs of the last two seasons it would not appear to be an area suitable for hopper development.

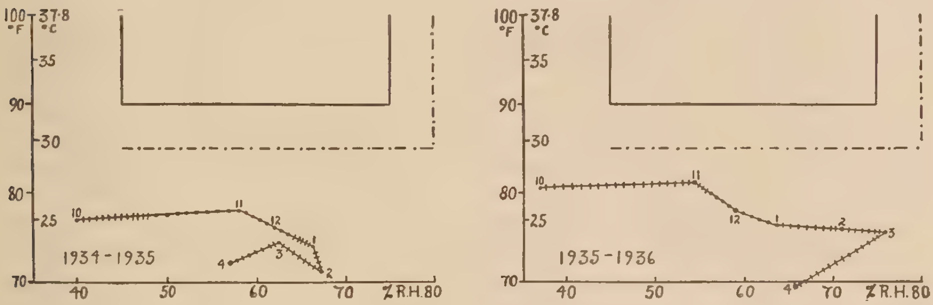

Fig. 9. Dedza.

Summary and Discussion.

A pronounced variation in the time taken by hopper bands of *Nomadacris septemfasciata*, Serv., to become adult swarms in different localities in the Nyasaland Protectorate during the four breeding seasons from 1932 to 1936, led to an investigation and comparison of certain climatic factors occurring during the critical months of hopper development at a number of stations where such variation had been particularly noticeable.

It was found that temperature and percentage relative humidity appeared to have considerable influence on the rate of development of the hopper bands, and that the quiescent nature of the bands in certain areas in some years, together with the unexpectedly small adult swarms that matured from these bands, seemed to be correlated with these same factors. It was noticeable that conditions during the first season, when development was generally normal, were somewhat hotter and drier throughout the country than in the later years and that, in most places, a marked increase in humidity usually accompanied by a decline in temperature was recorded each year up to 1936. In certain areas where hopper development occurred each year without much variation in length of time or intensity, such as the lower Shire River Valley, temperatures and humidity were found to have fluctuated only slightly from year to year.

Bioclimatographs of temperature and relative humidity for the critical months of hopper development for a series of four years at five different stations, together with less continuous records from four other stations, indicate that normal hopper development of this locust will occur, under natural conditions, at a mean maximum temperature of 85°F. (29·4°C.) and a mean relative humidity below 80 per cent. As the temperature increases to 90°F. (32·2°C.) or above and the humidity decreases to 75 per cent. or below, development becomes more rapid. The shortest recorded time of hopper development (56–60 days) occurred in the lower Shire Valley in the vicinity of Port Herald (fig. 1) in the season 1932–33, when the temperature was consistently greater than 90°F. (32·2°C.) and the humidity below 75 per cent.

At temperatures below 85°F. (29·4°C.) development is likely to be much prolonged, regardless of the relative humidity. Two records of hopper development taking over 100 days were obtained : at Likuni in the 1933–34 season, when the temperature was generally below 80°F., the humidity not being recorded ; and at Nkwale (fig. 4) in the 1934–35 season, when the temperature was considerably below 85°F., but the humidity ranged between 65 and 75 per cent.

Humidities greater than 80 per cent. also appear to inhibit hopper development (fig. 8, Mlanje).

Where temperatures in the region of 85°F. and a humidity of 70–75 per cent. occurred, the developmental period was between 75 and 85 days, approximately.

These records show agreement with the favourable conditions of temperature and humidity for hopper development as found experimentally by Hamilton (*l.c.*).

One high elevation station, Dedza, for two successive years gave a bioclimatograph (fig. 9) showing the mean maximum temperature to be almost consistently below 80°F. (26·7°C.) but with a reasonably favourable humidity, and though swarms passed through this area at a time when mating and egg-laying were taking place elsewhere, no breeding or development occurred here.

Although factors affecting the egg incubation period have not been considered (for reasons already explained, p. 417) it is, perhaps, worth noting that the period in which sexual maturation may be considered to occur in Nyasaland—October to December—is shown by the bioclimatographs, in most cases, to fall within the favourable temperature and humidity limits suggested by Hamilton (90°F. and 45–75 per cent. R.H.) in those areas where hopper development was normally straightforward, particularly in the lower Shire Valley (fig. 1). Where delayed hopper development occurred, a considerable portion of this same period is shown to be below the requisite temperature factor (figs. 3 and 4).

Certain inconsistent records must be mentioned. During the initial invasion of the country, in December 1932 and January 1933, when fully mature breeding swarms arrived and oviposited almost immediately, hopper bands developed in some areas in a normal manner in some 80 days, although during this period the temperature in these areas was sometimes considerably below the suggested minimum of 85°F. (fig. 7, Zomba). But such development was not repeated. Conversely, in the Fort Johnston area, at the south end of Lake Nyasa, the bioclimatographs (fig. 2) indicate that conditions would have been suitable for normal hopper development in all four years, and that the period of sexual maturation fell, for the main part, within the favourable range of temperature and humidity. In actual fact extensive breeding and normal development occurred here in the first two seasons. In the third season, 1934–35, although adult swarms were present at the time when breeding and egg-laying might have been expected, oviposition was unexpectedly light and hopper development almost negligible. In the fourth season, 1935–36, only one breeding swarm was recorded. This area generally experiences a rather low humidity during the greater part of the year, which may have had some influence on the paucity of breeding swarms occurring here immediately prior to the break of the rains.

Of the seven stations studied where locust breeding occurred, in this area alone hopper development failed under apparently suitable conditions, in one, perhaps two, of the four years.

In all cases, of course, the possibility must be considered of parent swarms, during the period of sexual maturation, being subject to climatic conditions differing from those recorded in the localities where egg-laying and hopper development actually takes place.

Acknowledgments.

The author wishes to acknowledge the invaluable assistance of Dr. B. P. Uvarov and Dr. A. G. Hamilton for their criticisms of this paper and suggestions for its improvement, and also to the former for his kindness in seeing it through the press.

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SEX RATIOS AND THE STATUS OF THE MALE IN PSEUDOCOCCINAE (HEM. COCCIDAE).

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1. Introduction.

The male sex in the family Coccidae is commonly supposed to play a quite minor part in the reproductive activity of this anomalous group of insects. The minuteness and fragility of the adult male, its complete dissimilarity to the female, its ephemeral existence, and the fact that cases of parthenogenesis have been proved to occur in the Coccidae, all tend to foster a supposition which is supported by little or no experimental evidence.

In the division of the Coccidae with which this paper treats, namely the Pseudococcinae, an examination of large natural aggregations of any of the commoner species almost invariably suggests that diploid parthenogenesis, in which the impaternate offspring consists entirely of females, must inevitably occur in order to account for the apparent vast preponderance of that sex. Moreover, this impression is strengthened by microscopic examination of breeding females, which reveals that embryonic development is partly or in certain species wholly completed before oviposition. Hence it is not surprising that sexual reproduction in the Pseudococcinae, as in the other divisions of the Coccidae, is considered to be of secondary importance.

In order to gain precise information concerning the importance of the male in reproduction and the relative proportions in which the sexes occur, extensive breeding experiments were carried out with four species of *Pseudococcus* and *Trionymus peregrinus*, Green, a species in a closely allied genus. The four species of *Pseudococcus* selected for study are among the commonest and most cosmopolitan in the genus, namely *P. citri*, Risso, *P. maritimus*, Ehr., *P. gahani*, Green, and *P. longispinus*, Targ.

The breeding experiments were carried out in the glasshouses of the Entomological Field Station of the University of Cambridge, and I must express my indebtedness to Dr. A. D. Imms, F.R.S., for the excellent facilities provided and for much constructive criticism during the course of the investigation.

I must also express my obligation to Mr. Harold Morrison, of the United States Bureau of Entomology, for confirming the identity of the species of mealy-bugs employed. Mounted specimens of all five species from material actually used in the experiments have been deposited in the United States National Collection of Coccidae. My thanks are also due to Mr. E. E. Green for the loan of type material of his species *Pseudococcus gahani* and *Trionymus peregrinus*.

2. The Sex Ratio.

The first step in the assessment of the importance of the male of *Pseudococcus* in reproduction was to ascertain beyond doubt that the females of the species were incapable of parthenogenesis. In carrying out the experiments designed for this purpose, involving the isolation of many virgin females, the object was not primarily the discovery of the phenomenon for the purpose of studying its mechanism in the group, but to carry out the inquiry on a scale sufficiently large to ascertain the presence or absence of this mode of reproduction, so that the importance of the male in the propagation of the species might be correctly evaluated. Apart from the fact that the females of many species of insects in which sexual reproduction normally occurs will reproduce parthenogenetically when denied fertilisation, complete assurance that impaternate offspring was absent was also necessary for the correct interpretation of sex ratio counts, and the precaution was amply justified in the case of the species *longispinus* in which unisexual families of females were produced by fertilised females.

The strictly zygogenetic nature of the reproductive process having been ascertained in the five species examined, the next step was to arrive at the relative proportions in which the sexes occur within each species, or in other words the sex ratio for each species. Now a sex ratio may be defined as the relative numerical proportion of the sexes within a group. The group may consist of a number of individuals of a given variety or species collected at random, or the progeny of a single female, or the sum of the progenies of a number of females of the same species. Whilst, of course, a sex ratio exists in bisexual species at all times, from the point of sex determination onwards geneticists recognise three conventional points at which it is customary to make determinations, namely, at conception, at birth and at maturity, and the ratios thus obtained are known as the primary, the secondary and the tertiary ratios respectively.

Determinations at conception and hatching are impracticable in *Pseudococcus*, because external sex characters are not then evident even in stained and mounted specimens and at maturity the males have dispersed in flight. Hence it is necessary to take counts of the males in the pre-pupal and pupal instars when cocoon formation has made the sex of the individual externally apparent, and it is not until late in the third instar that the female becomes externally unmistakable.

Determinations made at these times in species of *Pseudococcus* give close approximations to the ratio of the adults of both sexes prevailing in nature during the short period when the young unfertilised females are approaching maturity and the short-lived males are emerging, provided, of course, that no factor producing substantial differential sex mortality has been operative.

Sufficiently large sex counts of random collections of individuals have value in some species, especially the ratios occurring in natural populations from specified situations or circumscribed areas (the proportion of the sexes in *Pediculus* sp. from crops of head hair from tropical gaols is an interesting recent example of this type of sex ratio—*vide* Buxton[4]), but unless the collector is acquainted with the biology of the species concerned the results may be deceptive. *Pseudococcus* may be cited as a case in point, as the first two instars of both sexes closely resemble each other, and unless the collection is made during the brief pupal instars of the male the counts will show a very low proportion of that sex.

The sexing of the progeny of a single female, that is to say, the determination of what is called for convenience in this paper a family sex ratio, does not necessarily give an accurate index of the relative numerical proportion of the sexes prevailing in the species to which the female belongs, even though a full count is made of the progeny of an individual in which there has been no differential sex loss and in which the family is sufficiently large to be of undoubted statistical value.

In fact, such a determination may be seriously misleading in species in which the unisexuality of family progeny is prevalent, or in which several distinct types of family sex ratios are of normal occurrence; nor should it be forgotten that it is possible for occasional males or females to possess genetical constitutions productive of sex ratios widely different from those usual in their species. Furthermore, in this paper it will be shown that the primary sex ratios of females of both high and low fecundity in species of *Pseudococcus* are subject to considerable intra-specific variation.

The method adopted for ascertaining the specific sex ratios in *Pseudococcus* was to determine the family sex ratios of a series of females of each species sufficiently long to produce results of statistical significance, and the mean of each series of ratios was considered to be the sex ratio for the species (called for convenience the specific sex ratio) within the limits of a given standard error. This method has the advantage of disclosing such specific peculiarities of sex determination as may occur, and a much truer estimate is possible of the relative proportions of the sexes.

The factors which influence the sex ratio may be divided into two categories: those which control the primary ratio, and those which subsequently affect the primary ratio to produce secondary and tertiary ratios.

A primary sex ratio may be defined as the ratio at the time of sex determination; the secondary sex ratio is an indication of the extent of pre-natal differential mortality; and the tertiary ratio takes account in addition of further differential loss which may be incurred before the adult stage is attained.

With regard to the factors controlling the primary ratio it is commonly held that, provided that both kinds of gametes pertaining to the heterogametic sex are produced in equal numbers and are competitively equal to each other, that random segregation and fertilisation take place, and in the absence of inter-sexuality and unbalanced sex linked lethal factors, a 1 : 1 primary ratio of the sexes should occur. Owing to the number of physiological factors involved, however, it is not possible to predict the primary ratio from cytological data only, and even in the absence of known disturbing agencies it is probable that it deviates from parity more often and more widely than is suspected.

3. Experimental Methods.

The main desideratum in planning the breeding experiments was to secure species of host-plants which would sustain breeding females and their families, some of which numbered up to about four hundred, and at the same time withstand the high humidity to which they were unavoidably subjected during the course of the work.

Attempts to rear families of bugs from single females on unenclosed plants had to be abandoned because under glasshouse conditions predacious spiders and oviphagous mites increased in number so rapidly that sex ratio counts were rendered valueless.

The method finally adopted was one in common use in the laboratory of Dr. Imms. The plant was enclosed in an ordinary lamp-glass, the lower rim of which was sunk in fine sand which covered the soil in which the plant was growing. The upper opening of the glass was covered with cellophane, which proved a better material for this purpose than bolting silk and preserved a more equable temperature. The pots rested in earthenware saucers from which the plants obtained their water and the latter on permeating through the sand caused it to adhere to the lower rims of the lamp-glasses, and thus formed insect-proof chambers which served to prevent both the escape of bugs and the ingress of predators.

The evaporation from the wet sand, coupled with the moisture transpired from the plant, maintained the enclosed air at saturation point throughout the ranges of temperature employed. Unless the temperature of the air in the glass-house was fluctuating violently, that of the enclosed air in the lamp-glasses was variably higher to the extent of from 4°C. to 10°C.

All the species of mealy-bugs bred well under these conditions as soon as suitable hosts had been found, and considering the high humidity obtaining throughout, it was remarkable how few records were lost owing to the collapse of plants from disease. Counts of the sexes were only made from the progeny of isolated females which had been reared on carefully cleaned and enclosed plants. In the experiments concerned with parthenogenesis and delayed fertilisation, virgin females were enclosed under glass in a similar manner.

In *Pseudococcus* the most important factor controlling the number of progeny produced by each female is her potential fecundity, and this varied widely. Size is a partial but not a complete guide to fecundity. The wide variation in fecundity in individual females of the same species has also been observed in the few species in other divisions of the COCCIDAE in which counts of the progeny have been made. Thus, in *Coccus viride*, Green, a well known Lecaniid scale, the fecundity varies even more widely than in the five species of *Pseudococcus* studied in this paper,[5] for in *viride* the fecundity was found to vary from 50 to 580 progeny per female. It is possible, of course, that incomplete fertilisation or failure to complete oviposition may occasionally be responsible for small families, but it is impossible to detect them.

Losses from migration and parasitic and predatory activity in the experimental determination of the sex ratios were rendered practically negligible by the methods described above.

Microtome sections of *P. citri*, *P. maritimus*, and *P. longispinus* were cut for the cytological study of certain aspects of sex determination. For this purpose Carnoy's Fixative No. 2 formula and Heidenhain's iron haematoxylin stain proved satisfactory. Sections cut at 6 μ to 8 μ thick gave the best results.

4. **Pseudococcus citri,** Risso.

(*a*) *Parthenogenesis.*

Pseudococcus citri is almost certainly the commonest and most widespread representative of the genus, and besides being the centre of a small group of species which are only separable on slight morphological grounds, it seems likely that there are also a number of physiological strains. What is known with certainty is that aerial and root forms of the species exist, each of which will not survive in the habitat of the other, and it is not improbable that this lack of physiological identity within the morphological limits of the species as at present defined is responsible for a certain conflict of evidence with respect to its habits. Thus whilst Schrader[19] declares that *citri* reproduces strictly zygogenetically, Myers[16] claims to have reared two successive parthenogenetic generations from the species.

P. citri is almost polyphagous and occurs on a large number of hosts in conservatories and glass-houses, to which it is almost entirely restricted by climate in the North Temperate Zone, and both the aerial and the root strains were collected from hosts in the conservatory of the Cambridge Botanic Gardens. Inbred stocks of each strain initiated from single females were accumulated, the aerial strain on a species of *Coleus*, a hardy and very attractive host, and the root strain on a species of *Amaryllis*.

The first experiment undertaken was designed to ascertain whether virgin females of the aerial strain were able to reproduce parthenogenetically. Accordingly, 50 third instar females were isolated on each of ten *Coleus* plants, which were enclosed under glass in the manner already described to prevent the access of males.

The bugs were kept under daily observation from the beginning of the experiment on 21.i.36, and by 19.ii.36 all the females had passed through their final ecdysis except 26 which died, and this mortality was probably in large part due to injuries received in transference from the original host. The number of females was then well maintained until 24.ii.36, when evidence of ovisac formation by three females in Experiment No. 9, led to a close scrutiny of the plant and confining glass and two dead males were found. Within the next four days 33 females began to oviposit, and it is thought that the males had been introduced probably beneath females when the latter were transferred to the experimental plants.

However, none of the females isolated under the other lamp-glasses began the formation of ovisacs, and on 15.iv.36, the experiment was discontinued with the exception of Experiment No. 8, which was maintained in order to gain some indication of the longevity of virgin females. When this experiment was stopped on 6.viii.36, 22 females were still alive nearly eight months after the attainment of maturity, but none had begun even the external preliminary of oviposition, namely, the formation of an ovisac.

The following table summarises the results of the experiment, using ten plants :—

TABLE I.

No. 3rd instar ♀♀ placed on 21.i.36	No. adult ♀♀ counted on 19.ii.36	No. adult ♀♀ counted on 25.iii.36	No. adult ♀♀ counted on 15.iv.36	Date of termination of experiment
50	47	47	47	15.iv.36
50	50	49	49	,, ,,
50	45	45	44	,, ,,
50	48	48	48	,, ,,
50	50	50	50	,, ,,
50	48	46	45	,, ,,
50	42	41	41	,, ,,
50	48	48	48	6.viii.36
50	50	16	16	15.iv.36
50	46	46	46	,, ,,
500	474	436	434	

From this table it will be seen that 434 virgin females had lived 56 days from the attainment of the adult stage without breeding, although the usual length of the pre-oviposition period in this species when males have free access is in the neighbourhood of 10 days. The temperature recorded during the experiment ranged from 22·77°C. to 25·55°C., with a mean temperature for the period of 24·14°C., and the relative humidity was at 100 per cent. throughout the experiment.

On account of the breakdown of the experiment on Plant 9, and having gained a knowledge of the capacity of *Coleus* spp. to bear heavy infestations of *citri* for long periods in saturated air, it was decided to rear much larger numbers from the eggs of the progeny of females from Plant 9 and to eliminate the males after the formation of their pupal cocoons.

TABLE II.

Date of infestation (eggs)	Date first cocoon removed	Date last cocoon removed	Total ♂ cocoons removed	Adult ♀♀ present on 14.vi.36	Adult ♀♀ present on 14.vii.36	Adult ♀♀ present on 14.viii.36 when expt. terminated
15.iv.36	18.v.36	13.vi.36	234	*152	149	22
15.iv.36	15.v.36	21.vi.36	188	135	130	70
15.iu.36	15.v.36	19.vi.16	216	*397	392	9
15.iv.36	13.v.36	15.vi.36	84	190	185	8
15.iv.36	15.v.36	21.vi.36	276	*234	214	52
15.iv.36	15.v.36	19.vi.36	143	206	193	41
18.iv.36	13.v.36	11.vi.36	102	109	108	17
18.iv.36	13.v.36	14.vi.36	142	117	102	32
18.iv.36	13.v.36	15.vi.36	159	171	162	12
18.iv.36	13.v.36	14.vi.36	153	194	183	61
18.iv.36	13.v.36	15.vi.36	89	56	52	47
18.iv.36	13.v.36	11.vi.36	119	137	128	24
18.iv.36	15.v.36	24.vi.36	182	*234	218	31
18.iv.36	15.v.36	15.vi.36	140	*150	136	3
			2,227	2,482	2,352	429

* Virgin females removed for the experiments on delayed fertilisation.

Table II illustrates the work of this experiment, in which 2,482 virgin females, a number exclusive of those removed for the experiments on delayed fertilisation, had all died before 14.viii.36, with the exception of 429. None had oviposited. It is thought that the much lower longevity in this experiment as compared with that summarised in Table I is due to the autotoxic effect of large numbers crowded together on the host-plants. Nevertheless the great majority lived long after the normal pre-oviposition period of *citri*, but showed no indication of reproductive activity. The temperature range during this experiment varied from 21°C. to 26°C., with a mean for the period of 23°C. The relative humidity was again unvaried at 100 per cent. throughout.

The critical period during the above experiment was during the three weeks when the male cocoons were forming. A minute daily scrutiny of plants, lamp-glasses and cellophane caps, is then necessary to prevent the breakdown of the experiment, and this work consumed a lot of time. The transference of females in the third instar to clean host-plants, as was done in the previous and succeeding experiments of this kind, appears to be the better method of obtaining virgin females for this type of work, and in order to avoid inadvertently using young adult females which may have been fertilised it is necessary to examine each individual microscopically. The characters available to distinguish *living* third instar forms from young adult females are the longer and more slender antennae of the latter, for although the adult female has one more antennal segment than the third instar form, it is not usually possible to count the segments in life owing to the accumulation of debris thereon. The relatively greater length of the tibiae in relation to their tarsi in the adult is also a useful confirmatory character.

The root strain of *P. citri* was also tested for parthenogenetic reproduction, the host-plant used being Amaryllis (ten plants) and the results are tabulated in Table III.

TABLE III.

No. of 3rd instar ♀♀ started on 2.viii.36	No. adult ♀♀ on 16.viii.36	No. adult ♀♀ on 29.viii.36	No. adult ♀♀ on 11.ix.36	No. adult ♀♀ on 24.ix.36	No. adult ♀♀ on 7.x.36	No. adult ♀♀ on 20.x.36	No. adult ♀♀ on 3.xi.36 & date of termination of experiment
50	32	32	32	27	25	24	23
50	28	25	24	24	22	22	24
50	37	32	29	28	27	23	20
50	42	40	37	39	33	35	35
50	25	25	20	20	18	17	17
50	34	31	27	25	21	22	18
50	36	36	32	30	30	28	27
50	36	30	28	33	32	32	30
50	47	46	42	38	39	37	35
50	43	41	37	34	36	30	28
500	360	338	308	298	283	270	257

Thus, in the above experiment, out of 360 virgin females which moulted on or before 16.viii.36, 257 remained alive on 3.xi.36, when the experiment was terminated. During this period of 80 days no female produced offspring. The high mortality as compared with that shown in Table I was due to the losses incurred by being obliged to place the bugs at the base of the Amaryllis bulbs, and many died in the early stages. The range of temperature during this experiment varied from 22·4°C. to 27·3°C., with a mean for the period of 24·17°C. The relative humidity was 100 per cent. throughout the period of the experiment.

The results of the above experiments with virgin females of *citri*, taken in conjunction with those on delayed fertilisation in the same species and also with unpublished data concerned with the type of sex ratio produced by the postponement

TABLE IV.

A Series of 47 Family Sex Ratios of Pseudococcus citri, *Risso.*

Family group	Number of female	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of sex ratio in each family group ♂♂ per 100 ♀♀
Families varying from 351–404	1	206	191	397	107·85–	
	2	204	194	398	105·15–	
	3	193	184	377	104·89–	
	4	196	188	384	104·25+	
	5	178	185	363	96·21+	
	6	170	184	354	92·39–	
	7	190	214	404	88·75+	19·10–
Families varying from 301–350	8	166	140	306	188·57–	
	9	172	150	322	144·66+	
	10	169	172	341	98·25+	
	11	153	156	309	98·07+	
	12	155	167	322	92·81–	25·76–
Families varying from 251–300	13	137	114	251	120·175	
	14	133	118	251	112·71–	
	15	143	131	274	109·16–	
	16	156	143	299	109·09+	
	17	148	139	287	106·47–	
	18	140	134	274	104·47+	
	19	145	152	297	95·39–	
	20	132	139	271	94·96–	
	21	129	140	269	92·14–	
	22	121	132	253	91·66+	
	23	120	131	251	91·60–	
	24	137	155	292	88·38+	32·795
Families varying from 201–250	25	127	110	237	115·45–	
	26	113	99	212	114·14–	
	27	120	108	228	111·11–	
	28	129	118	247	109·32–	
	29	112	107	219	104·67–	
	30	119	118	237	100·84+	
	31	106	110	216	96·36–	
	32	119	125	244	95·20–	
	33	117	123	240	95·12–	
	34	109	113	222	94·69–	
	35	119	127	246	93·70–	21·75–
Families varying from 151–200	36	95	74	169	128·38–	
	37	98	90	188	108·88–	
	38	73	85	158	85·88–	42·50–
Families varying from 101–150	39	73	62	135	117·74–	
	40	56	67	123	83·58+	
	41	48	58	106	82·75+	34·99–
Families varying from 51–100	42	33	30	63	110·00–	
	43	46	43	89	106·97+	
	44	28	27	55	103·70–	
	45	26	29	55	89·65+	20·35–
Families varying from 0–50	46	20	20	40	100·00	
	47	18	20	38	90·00	10·00
Totals ...	—	5,697	5,606	11,413		

of fertilisation under conditions of low relative humidity, all seem to make it certain that the initiation of development in the eggs of *citri* is always dependent on the event of fertilisation.

(*b*) *The Sex Ratio.*

The specific sex ratio of *P. citri* was taken as the mean of the family sex ratios of a series of 47 females which are tabulated in Table IV. These ratios varied from 82·75+ to 128·38— ♂♂ per 100 ♀♀, and the sum of the progenies involved totalled 11,413, of which 5,606 were females and 5,697 were males.

Now let $x_1\ x_2 \ldots\ldots x_{47}$ = the family sex ratios of the females

Then $T = x_1 + x_2 \ldots x_{47} = 4776{\cdot}21$

Also $S = x_1^2 + x_2^2 \ldots x_{47}^2 = 490503{\cdot}2243$

Let the sum of the squares of the deviation from the mean = U

$$\text{Then } U = S - \frac{T^2}{n} = 490503{\cdot}2243 - \frac{22812181{\cdot}9641}{47}$$

$$= 490503{\cdot}2243 - 485365{\cdot}58$$

$$= 5137{\cdot}6443$$

Let s = the standard error.

$$\text{Then } s = \sqrt{\frac{u}{n\,(n-1)}} = \sqrt{\frac{5137{\cdot}64}{47\,(46)}} = \sqrt{\frac{5137{\cdot}64}{2162}}$$

$$= \sqrt{2{\cdot}38}$$

$$= 1{\cdot}54$$

Let $\bar{x}$ = the mean of the ratios $x_1\ x_2 \ldots\ldots x_{47}$

$$\text{Then } \bar{x} = \frac{T}{n} = \frac{4776{\cdot}21}{47} = 101{\cdot}62$$

∴ the specific sex ratio of *P. citri* = 101·62 ± 1·54♂♂ per 100♀♀.

My term "specific sex ratio" is rendered necessary by the fluctuating character of the family sex ratios in *Pseudococcus.* As applied to this group it may be defined as the relative numerical proportion of the sexes which prevails for a short period among the adults of the progeny of a group of females sufficiently numerous to have statistical significance. When the young females have just attained the adult stage and the short-lived males are emerging, their parents will be dead or moribund and the specific sex ratio will prevail for the few days in which the males survive, provided differential sex mortality has been negligible.

The maximum total progeny produced by any female of *citri* whose family sex ratio was determined was 404 and the lowest was 38. The average number of offspring per female worked out at 238·57+.

The range of temperature recorded during the determination of the family sex ratios of *citri* varied from 20·5°C. to 26·8°C., with a mean of 23·74°C. The relative humidity remained constant throughout at 100 per cent.

Six family sex ratios of the root strain of *citri* were also determined and they all fell within the range of the series from the aerial strain except one, which was only just outside the lower limit. Hence it seems probable that the specific sex ratio of the root strain would not be very different from that of the aerial one if a corresponding number of family ratios were counted.

(*c*) *The Fecundating Capacity of the Male.*

Since the specific sex ratio of *citri* has been shown to be in the region of parity, it follows that a very low number of matings per male would amply suffice to ensure the fertilisation of all the females. The maximum number of matings per male when single males were introduced on to plants infested with large numbers of virgin females enclosed under glass in the usual way was 23.

TABLE V.

A Series of Six Family Sex Ratios from Females of the Root Strain of Pseudococcus citri, *Risso.*

Male	Female	Total progeny	Family sex ratio ♂♂ per 100 ♀♀
123	114	237	107·89+
133	136	269	97·94+
65	69	134	94·20+
52	58	110	89·65−
130	153	283	84·96+
99	122	221	81·14+

The following is a record of the number of females fertilised by each of thirteen males :—7, 3, 17, 12, 0, 23, 14, 10, 2, 1, 17, 0, 2. These figures give an average of 9·07 females fertilised per male. The average of 9·07 females per male leaves no doubt that although reproduction is strictly zygogenetic there is always a sufficiency of males to fertilise all the females.

(*d*) *The Effect of Delayed Fertilisation on the Sex Ratio.*

The large number of virgin females made available by the experiments designed to detect parthenogenesis in *citri* provided useful material for examining the effect of delayed fertilisation on the sex ratio. Would female mealy-bugs whose fertilisation had been delayed long after the normal time breed and what alteration might be expected in the sex ratio of the offspring from such delayed matings?

At the time of the attainment of the adult stage the reproduction system of the female of *citri*, unlike that of the male, is undeveloped, but whether fertilisation then takes place or not, the ovaries grow rapidly and the dissection of females a few days after the final moult will reveal a large number of ova awaiting fertilisation. If, however, fertilisation takes place soon after the final moult, nearly all the eggs will have been fertilised *in situ*, and many of the contained embryos will have reached various stages of development before oviposition. However long they are kept, unfertilised females do not oviposit, and consequently they form a convenient vehicle for testing the effect of over-ripe eggs on sex determination.

From 40 females which were fertilised seven weeks after the attainment of the adult stage 36 produced offspring ; when the delay before fertilisation was increased to eight weeks 15 out of 30 proved fertile ; and when the period was extended to ten weeks, only 10 out of 30 oviposited.

This progressive increase of sterility with advancing age appears to be due to a differential longevity among the females, or in other words an increasing number of partly moribund ones. The following table gives a series of family sex ratios of 36 females whose fertilisation had been delayed for six weeks from the attainment of the adult stage.

TABLE VI.

A Series of Family Sex Ratios from 36 Females whose Fertilisation had been delayed for 42 Days.

Family groups (according to number of progeny)	Number of female	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of sex ratio in each family group ♂♂ per 100 ♀♀
Families varying from 351–400	1	228	163	391	139·87+	
	2	207	172	379	120·34+	19·53+
Families varying from 301–350	3	218	109	327	200·00–	
	4	185	117	302	158·11+	
	5	183	135	318	135·55+	64·45–
Families varying from 251–300	6	172	82	254	209·75+	
	7	191	93	284	205·37–	
	8	199	97	296	205·15–	
	9	172	85	257	202·35–	
	10	180	92	272	195·65–	
	11	179	93	272	192·47–	
	12	171	90	261	189·99–	
	13	183	105	288	174·28+	
	14	167	115	282	145·21+	
	15	152	107	259	142·05+	
	16	151	118	269	127·96+	31·79+
Families varying from 201–250	17	153	64	217	239·06–	
	18	142	64	206	221·875	
	19	163	74	237	220·70–	
	20	147	72	219	204·16+	
	21	132	71	203	185·91–	53·15–
Families varying from 151–200	22	110	45	155	244·44–	
	23	113	47	160	240·425	
	24	114	76	190	150·60	
	25	92	64	156	143·75–	
	26	102	89	191	114·60+	129·84–
Families varying from 101–150	27	89	54	143	164·81–	
	28	72	48	120	150·00–	14·81–
Families varying from 51–100	29	41	18	59	227·77+	
	30	37	17	54	217·64+	
	31	54	25	79	216·00–	
	32	38	20	58	190·00–	
	33	57	32	89	178·125	
	34	37	23	60	160·86+	
	35	29	24	53	120·87–	106·94+
Families varying from 0–50	36	23	13	36	176·92–	
Totals		4,683	2,713	7,396		

The mean of the sex ratios

$$= \bar{x} = \frac{T}{n} = \frac{6511\cdot97}{36} = 180\cdot89 ♂♂ \text{ per } 100 ♀♀$$

Sum of the squares of the deviations from the mean $= U = S - \frac{T^2}{n}$

$$= 1226401{\cdot}6906 - 42405753{\cdot}28/36$$
$$= 1226401{\cdot}6906 - 1177937{\cdot}6$$
$$= 48464{\cdot}1$$

The standard error $= s = \sqrt{\frac{U}{n\,(n\text{-}1)}} = \sqrt{\frac{48464{\cdot}1}{36\,(35)}} = \sqrt{\frac{48464{\cdot}1}{1260}}$

$$= \sqrt{38{\cdot}46} = 6{\cdot}20$$

∴ the mean of the family sex ratios of 36 females whose fertilisation had been delayed for six weeks is 180·89 ± 6·20♂♂ per 100♀♀.

Thus it is seen that a delay of six weeks in the time of mating altered the mean sex ratio of the progeny from 101·62 ± 1·54 to 180·89 ± 6·20♂♂ per 100♀♀. The average number of progeny per female fell from 225·95+ from 47 females fertilised at the normal time to 205·44+ from 36 females whose fertilisation was postponed for six weeks. The environmental conditions varied little from those obtaining in the experiments where mating occurred at the normal time. Since the bugs in both series of determinations were enclosed under lamp-glasses in the usual manner, the relative humidity remained at 100 per cent. throughout. The temperature range recorded in the delayed matings varied from 19·50°C. to 24°C., with a mean of 23°C., or only 0·74°C. higher than the mean temperature at which the progeny from the normal matings were bred.

Table VII gives a series of family sex ratios of fifteen females whose fertilisation was delayed eight weeks from the attainment of the adult stage.

TABLE VII.

A Series of Family Sex Ratios of 15 *Females whose Fertilisation had been delayed* 56 *days* (8 *weeks*).

Family groups (according to number of progeny)	Number of female	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of sex ratio in each family group ♂♂ per 100 ♀♀
Families varying from 351–406	1	270	84	354	321·98–	
	2	305	101	406	301·98–	20·00–
Families varying from 251–300	3	217	56	273	387·50–	
	4	210	65	275	323·07+	
	5	203	77	280	263·63+	123·87–
Families varying from 201–250	6	181	63	244	287·30–	
Families varying from 151–200	7	152	40	192	380·00–	
	8	129	34	163	379·41–	
	9	153	47	200	325·53–	
	10	136	42	178	323·80+	56·20–
Families varying from 101–150	11	91	26	117	358·00–	
	12	104	30	134	346·66+	
	13	78	31	109	251·61–	106·39–
Families varying from 51–100	14	50	13	63	384·50–	
	15	47	17	64	276·47–	108·03–
Totals ...	—	2,326	726	3,052		

The mean of the sex ratios

$$= \bar{x} = \frac{T}{n} = \frac{4910\cdot99}{15} = 327\cdot40 \text{ ♂♂ per } 100 \text{ ♀♀}$$

The sum of the squares of the deviations from the mean $= U = S - \frac{T^2}{n}$

$$= 1636248\cdot7083 - \frac{24117822\cdot7801}{15}$$

$$= 1636248\cdot7083 - 1607854\cdot852 = 28393\cdot856.$$

The standard error $= s = \sqrt{\frac{U}{n\ (n\text{-}l)}} = \sqrt{\frac{28393\cdot856}{15\ (14)}} = \sqrt{\frac{28393\cdot856}{210}}$

$$= \sqrt{135\cdot21} = 11\cdot63$$

∴ the mean of the sex ratios of fifteen females whose fertilisation was delayed for 8 weeks is 327·40 ± 11·63♂♂ per 100♀♀.

The fecundity only fell slightly compared with females which were mated after six weeks, and the average number of progeny per female was 203·46+.

The following table records a series of family sex ratios whose fertilisation was delayed ten weeks from the attainment of the adult stage.

TABLE VIII.

A series of ten Family Sex Ratios from Females of P. citri *whose Fertilisation had been delayed 70 Days from the Attainment of the Adult Stage.*

Family groups (according to number of progeny)	Number of female	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation in the sex ratio in each family group ♂♂ per 100 ♀♀
Families varying from 251–300	1	240	53	293	452·82—	
	2	231	52	283	444·23—	8·59—
Families varying from 201–250	3	197	20	217	985·00—	
	4	172	39	211	441·02+	544·98—
Families varying from 151–200	5	158	36	194	438·88+	
	6	157	37	194	424·44—	14·44+
Families varying from 101–150	7	110	25	135	440·00—	
	8	86	21	107	409·52—	30·48—
Families varying from 0–100	9	51	1	52	5100·00	
	10	31	4	35	775·00—	4325·00—
Totals ...	—	1,433	288	1,721		

The mean of the sex ratios

$$= \bar{x} = \frac{T}{n}\ \frac{9910\cdot91}{10} = 991\cdot091$$

The sum of the squares of the deviations from the mean $= U = S - \frac{T^2}{n}$

$$= S - \frac{98226137\cdot0281}{10} = 28911806\cdot4841 - 9822613\cdot7028.$$

$$= 19089192\cdot7813$$

The standard error $= s = \sqrt{\frac{U}{n(n-l)}} = \sqrt{\frac{19089192{\cdot}7813}{90}} = \sqrt{21202{\cdot}142}$
$= 460{\cdot}5$

∴ the mean of the sex ratios of ten females whose fertilisation was delayed for 10 weeks is 991·091 ± 460·5♂♂ per 100♀♀.

The high standard error is occasioned by the abnormally high sex ratio of Female No. 9, in whose progeny only one female occurs. The number of progeny per female fell to 172·10, or 53·85 per head less than those for females fertilised at the normal times.

When a variation in the sex ratio is alleged to be indicative of a change of sex, the objection is almost invariably raised that what is being measured is an undetected differential mortality and that the sex of no individual has really been changed. Notwithstanding the possibility of this factor having played some part, the violent disturbance of the family sex ratios of 62 females, all in the same direction, and which had been bred under almost the same conditions as those under which normal ratios had been obtained, cannot be disposed of by such an explanation.

An examination of the literature reveals that this type of disturbance in the sex ratio is not an isolated case of the kind, since the phenomenon has been proved to occur in several classes of vertebrates, although this is apparently the first case in which it has been clearly demonstrated in the invertebrates. It is true that Barnes[2] records an increase in the proportion of males in the sex ratios of *Dasyneura arabis*, Barnes (CECIDOMYIIDAE) following a delay of 48 hours before mating, but the recorded increase was on the borderline of significance and a longer delay, if that were feasible in *D. arabis*, might have raised the increase of males well beyond the limits of chance fluctuation.

In the Amphibia, Hertwig[9] demonstrated in the frog that the sex ratio of late fertilised zygotes gave a much higher proportion of males. Kuschakewitsch[13] repeated Hertwig's experiments and showed quite clearly that the result was not due to differential mortality, and Mrsic[15] also proved that a similar phenomenon may occur in the trout.

In fishes and Amphibia delay in fertilisation is associated with absorption of water by the ova, whilst conversely King[11] has shown that by keeping the eggs of *Bufo* out of water for some hours after their fertilisation, during which period they normally absorb water, the proportion of females can be increased from 50 per cent. to 80 per cent. It may be mentioned in connection with the relation of the water content of the ova to the determination of sex that Riddle[17] has produced considerable evidence that in the case of the pigeon higher water values are associated with male-producing eggs. It would be of interest to know whether the increased proportion of males in the sex ratios of late fertilised zygotes in *Pseudococcus* is associated with the absorption of water by the ova in the oviducts during the long wait before fertilisation. In view of the fact that these experiments were carried out under conditions of high humidity, an experiment is in progress in which the air in which the plants and insects are growing is being maintained at a very low humidity.

The effect produced on their sex ratios by the greatly increased elimination of water from the insects during the period prior to fertilisation may be significant.

The increased proportion of males among late fertilised zygotes has been explained theoretically on the assumption that in cases where the female is the homogametic sex, the over-ripeness of the ova results in primary non-disjunction of the X chromosomes and their extrusion into the polar body, thus leading to the production of males. Light might be thrown on the validity of this theory by examining the results of delayed fertilisation on the sex ratio of an animal in which the female is the heterogametic sex, and a species of moth is now being bred for this purpose.

There are certain theoretical difficulties in accepting non-disjunction as the cause of the altered sex ratio in late fertilised zygotes of *Pseudococcus*, as the sex gene bearing chromatin is probably distributed among a number of chromosomes.

Five chromosomes in the male are closely associated and behave in certain respects like a hetero-chromosome, and since the latter forms the entire nuclear chromatin of half the spermatozoa evolved, it is clear that they must form about half the chromosome complement of many females. However, if non-disjunction does play a part in the increased proportion of males, it follows that there should be a number of males with the sex chromosome constitution analogous to OX males in *Drosophila*, and these may be sterile.

A large number of males from the abnormal sex ratios were examined and all appeared to be normal externally, and a few (12) which were tested, proved fertile. Owing to pressure of work in connection with other experiments then in progress, an examination of the internal anatomy and more numerous tests for cases of sterility had to be postponed.

Females employed in delayed fertilisation experiments were always mated to newly emerged males. Unlike the ova, the spermatozoa in *Pseudococcus* are mature on the attainment of the adult stage, but it is impossible to test the effect of over-ripe spermatozoa on the sex ratio owing to the fact that the male lacks mouth-parts and dies within a few days of emergence.

5. **Pseudococcus maritimus,** Ehr.

Pseudococcus maritimus has a world-wide distribution and, like *citri*, may be regarded as the representative of a group within the genus. Like most Pseudococcine forms it is polyphagous and is not uncommon under glass in this country, and although the species was subsequently collected in the vicinity of Cambridge, the writer is indebted for the original colony utilised for these experiments to the late Mr. Maldwyn Davies of the Agricultural College, Bangor, N. Wales.

The original host-plant was vine, but cuttings of the latter proved unsuitable for the experimental breeding of the bugs ; similarly, *Primula sinensis*, on which it is reputed to thrive, was also tried, but this host failed to withstand the moist conditions. An attractive host which withstood well the high humidity was finally found in the common potato plant (*Solanum tuberosum*).

Like those of *citri* the virgin females of *maritimus* failed to reproduce parthenogenetically when kept under conditions which would have forced a display of this type of reproduction had the potentiality been there. Third instar females were isolated on ten plants and enclosed in the same way as for the experiments on *citri*, and then kept under daily observation. Counts were made at fortnightly intervals and Table IX summarises the results of the experiment.

The following table shows that out of 411 virgin females counted on 30.vi.36 and maintained in isolation from the male, only 54 remained alive on 23.ix.36 after a period of 85 days, and these survivors showed every sign of old age or moribundity. Despite the fact that no female bred, a peculiarity was that all of them produced voluminous white cottony ovisacs which contained no ova or only a few infertile ones. The range of temperature recorded during the experiment varied from 20·11°C. to 25·54°C., with a mean of 22·95°C., whilst in common with all the experiments conducted on enclosed plants the relative humidity was 100 per cent. throughout the range of temperature recorded.

TABLE IX.

No. of 3rd instar females placed on plant	Virgin ♀♀ counted on 30.vi.36	Virgin ♀♀ counted on 14.vii.36	Virgin ♀♀ counted on 28.vii.36	Virgin ♀♀ counted on 11.viii.36	Virgin ♀♀ counted on 25.viii.36	Virgin ♀♀ counted on 9.ix.36	Virgin ♀♀ counted on 23.ix.36
50	37	37	37	36	32	22	7
50	45	44	43	42	37	28	8
50	44	43	43	42	40	17	12
50	38	38	38	36	23	7	4
50	41	36	36	36	25	11	0
50	34	32	32	30	17	12	9
50	45	45	45	41	32	23	13
50	48	48	42	41	40	5	2
50	43	41	35	33	22	18	6
50	36	32	10	10	8	8	3
500	411	396	361	347	276	151	64

(*a*) *The Sex Ratio.*

The family sex ratios of *P. maritimus* from which the specific sex ratio is determined showed a wider divergence than in any other species examined, varying from 8·69— to 377·77+♂♂ per 100♀♀ from a series of 42 females. This wide divergence is to a large extent due to six ratios which show a higher proportion of males than females, especially that of Female No. 33. On the other hand, it should be noted that the remaining 36 ratios are all below 76·00♂♂ per 100♀♀, and there appears to be no doubt that the apparent absence of males, so characteristic of this group, is to some extent a real one in this species. The following table consists of a series of family sex ratios of *maritimus*.

TABLE X.

A Series of 42 Family Sex Ratios of P. maritimus.

Family groups (according to number of progeny)	Number of female	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of sex ratios in family group ♂♂ per 100 ♀♀
Families varying from 201–251	1	79	152	231	51·97+	
	2	67	141	208	47·51+	
	3	48	184	232	26·08+	25·89+
Families varying from 151–200	4	78	111	189	70·27—	
	5	72	114	186	63·15+	
	6	61	98	159	62·24—	
	7	66	121	187	54·54—	
	8	61	113	174	53·18—	
	9	50	108	158	46·29+	
	10	54	119	173	45·38—	
	11	54	122	176	44·26—	
	12	51	123	174	41·46—	28·81—

TABLE X—*Continued.*

Family groups (according to number of progeny)	Number of female	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of sex ratios in family group ♂♂ per 100 ♀♀
Families varying from 101–150	13	46	61	107	75·40+	
	14	46	69	115	66·66+	
	15	60	90	150	66·66+	
	16	44	98	142	44·89−	
	17	37	90	127	41·11−	
	18	36	97	133	37·11−	
	19	26	75	101	34·66−	
	20	25	82	107	30·48+	
	21	32	109	141	29·35+	
	22	20	86	106	23·25−	
	23	24	111	135	21·62−	53·78−
Families varying from 51–101	24	48	31	79	154·83+	
	25	48	32	80	150·00−	
	26	45	40	85	112·50−	
	27	29	40	69	72·50−	
	28	21	49	70	42·85+	
	29	21	60	81	35·00−	
	30	15	77	92	19·47+	
	31	12	69	81	17·38+	
	32	9	80	89	11·25−	143·58+
Families varying from 0–50	33	34	9	43	377·77+	
	34	25	21	46	119·04+	
	35	17	15	32	113·33−	
	36	3	5	8	60·00−	
	37	3	8	11	37·50−	
	38	8	22	30	36·36−	
	39	8	30	38	26·66−	
	40	7	34	41	20·58+	
	41	2	18	20	11·11−	
	42	2	22	24	8·69−	369·08−
Totals ...	—	1,494	3,136	4,630		

The specific sex ratio $= \bar{x} = \frac{T}{n} = \frac{2505{\cdot}14}{42} = 59{\cdot}65$

The sum of the squares of the deviation from the mean $= U = S - \frac{T^2}{n}$

$$= 301500{\cdot}2054 - \frac{6275726{\cdot}4196}{42}$$

$$= 301500{\cdot}2054 - 149422{\cdot}0576$$

$$= 152078{\cdot}1478.$$

The standard error $= s = \sqrt{\frac{U}{n\,(n\text{-}1)}} = \sqrt{\frac{152078{\cdot}15}{42\ (41)}} = \sqrt{\frac{152078{\cdot}15}{1722}}$

$$= \sqrt{88{\cdot}315} = 9{\cdot}398$$

∴ The specific sex ratio of *P. maritimus* $= 59{\cdot}65 \pm 9{\cdot}398$.

The average number of progeny per female $= \frac{4630}{42} = 110{\cdot}24$, a number less than half that per female of *citri*.

The range of temperature recorded during the above experiment varied from 18·5°C. to 24·37°C., with a mean temperature of 21·77°C. for the period.

Now what is the cause of the much lower specific sex ratio of *maritimus* as compared with *citri*, or rather why do the vast majority of the family sex ratios of *maritimus* lie below 76·00♂♂ per 100♀♀?

We are indebted to Schrader[18, 19] for several cytological studies of species of *Pseudococcus*, and he found that oogenesis and spermatogenesis are similar in these two species in all essential details.

The diploid number of chromosomes in both sexes is ten. In the male the nuclei of all resting cells show a clump of densely staining chromatin, as well as more lightly stained and flocculent chromatin scattered throughout the nuclei. Resting cell nuclei in the female show the chromatin in flocculent masses with no suggestion of clumping. In the prophases of the first spermatocyte division of *citri* and *maritimus* five chromosomes are evolved considerably in advance of the remaining five. These chromosomes first evolved have a tendency to clump in the case of *maritimus*, but the tendency is less marked and occasionally absent in *citri*.

The first spermatocyte division is equational, ten chromosomes going to each pole, and there is evidence that the grouping of the chromosomes previously observed persists in the daughter cells.

The second spermatocyte division follows without a regular interkinesis, and apparently the five clumped chromosomes go to one pole and the remaining five to the other pole. This is the reduction division, and the massed group of chromosomes has its fibres formed in a perfectly normal manner. The spindle fibres for the loose group are, however, formed later, and in an irregular manner, and although the members of this group all go to the same pole, there is a noticeable lack of co-ordination among them.

The distribution of the chromosomes in the reduction is not accompanied by a cytoplasmic division. Each cell is a double spermatid which gives rise to two spermatozoa, one with the massed group of five chromosomes and one with the loose group of five chromosomes.

In the female, all ten chromosomes are evolved simultaneously, five tetrads are formed and reduction is normal. From these facts it is inferred that the female is homozygous for sex, but that the evidence is obviously insufficient to determine whether the female is homozygous for the massed or the loose group of chromosomes since, as Schrader[18] has pointed out, failure of the chromosomes in the cells of the female to show any massing is not necessarily an indication that the spermatozoa carrying the loose group are female producing. All such exceptional behaviour may well disappear in the presence of the homozygous mate of each chromosome.

The present writer made a close study of the spermatids in both species, but was unable to observe any sign of degeneration within them in either species which would have suggested a differential production of gametes.

The wide disparity between the specific sex ratios of *citri* and *maritimus*, despite close cytological similarity, is an indication of the danger of attempting to predict the sex ratio on purely cytological data. Experimental evidence is also required.

6. Pseudococcus gahani, Green.

Pseudococcus gahani became a well-known species many years ago in consequence of its great increase in numbers in the citrus groves of California following its introduction into that State from Australia. It is also not uncommon in Europe under glass, and I found it growing on *Datura* spp. in the Cambridge Botanic Gardens, and *Datura stramonium* proved a good experimental host, since the Solanaceae vie with the Rutaceae in providing favourable food-plants for this species.

It was demonstrated in the same manner as for *citri* and *maritimus* that the ova of *gahani* are unfailingly zygogenetic in development. The following table summarises the work of the experiment with ten different plants.

TABLE XI.

Number of 3rd instar females placed on 17.viii.36	Adult virgin ♀♀ counted on 31.viii.36	Adult virgin ♀♀ counted on 14.ix.36	Adult virgin ♀♀ counted on 28.ix.36	Adult virgin ♀♀ counted on 12.x.36	Adult virgin ♀♀ counted on 26.x.36	Adult virgin ♀♀ counted on 9.xi.36	Adult virgin ♀♀ counted on 23.xi.36	Adult virgin ♀♀ counted on 7.xii.36
50	50	48	46	46	40	34	30	28
50	47	47	47	47	38	31	31	29
50	39	38	38	37	32	27	26	25
50	48	48	46	46	45	33	31	31
50	47	43	43	42	28	26	23	20
50	45	43	41	41	34	34	32	28
50	47	46	46	45	41	40	29	29
50	48	48	44	40	38	31	27	25
50	49	46	46	46	35	29	28	27
50	50	50	48	46	40	32	26	23
500	470	457	445	436	371	317	283	265

Table XI shows that out of 470 adult virgin females which underwent their final moult on or about 31.viii.36, 265 were still alive 88 days later on 7.xii.36, when the experiment was discontinued. The normal pre-oviposition period for this species is about 12 days. The surviving specimens were showing indications of old age, but neither they nor those which had died produced offspring.

The range of temperature recorded from daily observations during the experiment varied from 19·4°C. to 24·7°C., with a mean for the period of 22·5°C. The enclosed air surrounding the host-plants remained saturated during the whole range of temperatures recorded for the period of the experiment.

(*a*) *The Sex Ratio.*

P. gahani resembles *citri* very closely in its reproductive powers, and a series of 61 family sex ratios were determined which are set out in Table XII.

TABLE XII.

A Series of 61 Family Sex Ratios of P. gahani.

Family groups (according to number of progeny)	Number of female	Males	Females	Total progeny	Family sex ratios ♂♂ per 100 ♀♀	Maximum variation of sex ratios in family group ♂♂ per 100 ♀♀
Families varying from 351–406	1	171	234	405	73·07+	
	2	168	230	398	73·04+	
	3	134	234	368	57·26−	
	4	104	270	374	38·51+	
	5	100	273	373	36·63−	
	6	82	324	406	25·30+	47·77+
Families varying from 301–350	7	133	204	337	65·19+	
	8	117	199	316	58·79−	
	9	102	245	347	41·63−	24·56+

TABLE XII—*Continued.*

A Series of 61 Family Sex Ratios of P. gahani.

Families varying from 251–300	10	93	165	258	56·36—	
	11	94	180	274	52·22—	
	12	79	177	256	44·62+	
	13	76	178	254	42·69+	
	14	84	214	298	39·25—	
	15	58	212	270	27·35+	
	16	49	238	287	20·59—	35·77—
Families varying from 201–250	17	95	128	223	74·21+	
	18	91	130	221	70·00—	
	19	83	124	207	66·93+	
	20	88	133	221	66·16—	
	21	75	143	218	52·44+	
	22	60	151	211	39·73—	
	23	68	175	243	38·85+	
	24	65	170	235	38·23—	
	25	62	166	228	37·34+	
	26	56	167	223	33·53—	
	27	41	162	203	25·30+	
	28	55	162	217	33·95—	48·91+
Families varying from 151–200	29	79	81	160	97·53—	
	30	72	105	177	68·57—	
	31	69	101	170	68·31—	
	32	78	118	196	66·10—	
	33	58	106	164	54·71+	
	34	53	127	180	41·73—	
	35	50	144	194	34·72—	
	36	41	121	162	33·88—	
	37	33	136	169	24·26—	
	38	30	128	158	23·43+	
	39	34	160	194	21·25—	75·28—
Families varying from 101–150	40	43	84	127	51·19—	
	41	44	96	140	45·83—	
	42	40	97	137	41·23+	
	43	36	90	126	40·00—	
	44	33	90	123	36·66+	
	45	26	83	109	31·32—	
	46	32	113	145	28·32—	
	47	24	107	131	22·43+	
	48	22	102	124	21·56+	
	49	21	110	131	19·09—	
	50	20	117	137	17·09—	
	51	15	99	114	15·15—	36·04—
Families varying from 51–100	52	28	50	78	56·00—	
	53	35	63	98	55·55—	
	54	35	64	99	54·68+	
	55	25	57	82	43·86—	
	56	30	70	100	42·86—	
	57	14	43	57	32·55+	
	58	14	47	61	29·78+	
	59	19	72	91	26·38+	
	60	18	72	90	25·00—	
	61	19	78	97	24·35+	31·65—
Totals ...	—	3,673	8,519	12,092		

The specific sex ratio $= x = \frac{T}{n} = \frac{2624{\cdot}54}{61} = 43{\cdot}025$

The sum of the squares of the deviations from the mean $= U = S - \frac{T^2}{n}$

$= 131920{\cdot}9494 - 112921{\cdot}48 = 18999{\cdot}47$

The standard error $= s = \sqrt{\frac{U}{n\ (n\text{-}1)}} = \sqrt{\frac{18999{\cdot}47}{61\ (60)}} = \sqrt{\frac{18999{\cdot}47}{3660}}$

$= 2{\cdot}28$

$\therefore$ the specific sex ratio of *P. gahani* = 43·025 = 2·28.

The average number of progeny per female is $\frac{12092}{61} = 198{\cdot}18+$ and the maximum number of offspring produced by any female in the above species is 406 and the minimum 57. The temperature range varied from 18·45°C. to 24·2°C. with a mean of 22·33°C. for the duration of the experiment. The relative humidity was 100 per cent. throughout. The family sex ratios vary from 15·15— to 97·53— ♂♂ per 100♀♀, and the most interesting and important feature of this series is the very wide divergence of the sex ratios of females, the numbers of whose progenies lie in the neighbourhood of the maximum for the species, with the consequence that the factor of differential sex loss from whatsoever cause arising cannot be held accountable for the huge variations.

7. **Pseudococcus longispinus,** Targ.

Pseudococcus longispinus is a relatively large species recognised by the elongate body, the vitreous waxy filaments which protrude here and there from the body surface, and the long tassels of wax which are attached to the anal margin of the body.

It is the type species of the genus and of general distribution, and in relation to the subject matter of this paper it presents a feature of special interest, since embryonic development is entirely completed within the body of the female. This suggests that if it were necessary to select species of *Pseudococcus* in which parthenogenesis appears more probable than in others, those species which exhibit viviparity or have a short period of external incubation of the egg would be obvious choices.

Breeding experiments with this species presented certain unexpected difficulties. Owing to the known partiality of *longispinus* for nearly all species of ferns, it was assumed that they would prove excellent experimental hosts. Four species of ferns were tried, but on all of them the bugs failed to thrive satisfactorily when enclosed under glass. It appears that transpiration in ferns is more active than in many other plants, and that the somewhat copious condensation of moisture on the fronds occasioned by the enclosed conditions militated against the well-being of the bugs.

After several hosts had been tried, the potato plant, *Solanum tuberosum,* was found to meet all requirements. The preliminary experiment designed to detect parthenogenesis, using ferns as a host, was only partly successful, because from the progeny of 30 females, each of which was isolated on species of *Asplenium* under glass on 25.x.35, only 12 adult females were obtained a month later. These were kept until 14.i.36, on which date they were sectioned. No embryos could be detected in any of the specimens, and in three cases the ovaries were obviously degenerating.

Another experiment, using potato plant as a host, met with greater success and the results are summarised in Table XIII.

TABLE XIII.

Third instar ♀♀ present on 19.i.36	Adult virgin ♀♀ present on 1.ii.36	Adult virgin ♀♀ present on 15.ii.36	Adult virgin ♀♀ present on 29.ii.36	Adult virgin ♀♀ present on 14.iii.36	Adult virgin ♀♀ present on 28.iii.36	Adult virgin ♀♀ present on 11.iv.36	Adult virgin ♀♀ present on 25.iv.36	Adult virgin ♀♀ present on 9.v.36	Adult virgin ♀♀ present on 25.v.36
50	42	42	40	36	36	34	34	34	32
50	49	45	44	40	40	37	35	31	31
50	50	40	40	39	36	20	19	19	17
50	35	35	35	35	34	32	29	28	28
50	42	41	39	36	32	32	31	29	29
50	47	43	43	41	37	34	34	34	31
50	38	37	36	36	34	32	25	23	23
50	43	40	39	38	35	33	30	30	30
50	50	48	47	45	40	37	35	35	32
50	46	42	40	38	32	26	31	30	30
500	442	413	403	384	356	317	303	293	283

From the above table it will be seen that from 442 adult virgin females newly moulted on or before 1.ii.36, 283 were still alive 103 days later on 25.v.36, when the experiment was terminated, but no female had produced offspring. The duration of the pre-oviposition period in this species, when males have free access, is in the neighbourhood of 16 days.

The range of temperature recorded from daily observations during the above experiment varied from 22·4°C. to 25·34°C., with a mean of 23·94°C. The relative humidity was constant at 100 per cent. throughout the experiment.

(*a*) *The Sex Ratio.*

The method of oviposition pursued by females of *longispinus* was a factor which increased the difficulty of determining sex ratios in the species. Instead of the female laying her ova *en masse* on one site in a relatively short interval of time (a method common in the genus), she laid a batch of eggs numbering up to about fifty on one site and then migrated before continuing oviposition after an uncertain interval of time. This intermittent habit of oviposition proved inconvenient, since as often as not the female migrated off the plant on to the walls of the enclosing glass, where the progeny, which hatched almost immediately, dispersed rapidly in the absence of food, and many more observations were needed to carry through the work successfully.

The females of *longispinus* also proved remarkable in producing both bisexual and unisexual families. The unisexual families consisted entirely of females, and in the sex ratios from the bisexual families the proportion of males was low. Below is tabulated a series of nineteen family sex ratios from which the specific sex ratio for bisexual families has been computed.

TABLE XIV.

Family groups (according to number of progeny)	Number of female	Males	Females	Total progeny	Family sex ratios ♂♂ per 100 ♀♀	Maximum variation of sex ratios in family group ♂♂ per 100 ♀♀
Families varying from 351–400	1	71	327	398	21·71—	
	2	50	320	370	15·62—	
	3	42	348	390	12·06+	9·65—
Families varying from 251–300	4	36	260	296	13·84+	
	5	32	234	266	13·675+	
	6	27	257	284	10·50+	3·34+
Families varying from 201–250	7	41	203	244	20·19+	
Families varying from 151–200	8	37	150	187	24·66+	
	9	30	135	165	22·22+	
	10	24	135	159	17·77+	
	11	23	132	155	17·42—	
	12	22	129	151	17·05—	
	13	24	144	168	16·66+	
	14	22	132	154	16·66+	
	15	23	143	166	16·08—	
	16	15	154	169	9·74—	14·92—
Families varying from 101–150	17	45	81	126	55·55—	
	18	21	123	144	17·07—	38·48+
Families varying from 51–100	19	20	72	92	27·77+	
Totals ...	—	605	3,479	4,084		

The specific sex ratio = the mean of the family sex ratios $= \bar{x} = \frac{T}{n} = \frac{366\cdot24}{19}$

$= 19\cdot28$

The sum of the squares of the deviations from the mean $= U = \frac{S - T^2}{n}$

$= 8825\cdot7340 - 7059\cdot56 = 1766\cdot17$

The standard error $= s = \sqrt{\frac{U}{n\,(n\text{-}1)}} = \sqrt{\frac{1766\cdot17}{19/18}} = \sqrt{\frac{1766\cdot17}{342}}$

$= \sqrt{5\cdot164} = 2\cdot27$

∴ the specific sex ratio of the bisexual families of *longispinus* = 19·28 ± 2·27.

The range of temperature recorded during the breeding of the bisexual and unisexual families of *longispinus* varied from 21·70°C. to 27°C., with a mean temperature for the period of 24·45 per cent. The relative humidity was at 100 per cent. throughout.

The average number of progeny in bisexual families was $\frac{4084}{19} = 214\cdot94+$. The maximum number of progeny produced by any female was 398 and the minimum 92.

(*b*) *Unisexual Families.*

A number of fertilised females of *longispinus* produced families consisting entirely of females and despite the fact that the total of individuals in each unisexual family is low compared with those for bisexual families, experimental experience on this subject enables me to state that to obtain even 32 females, which is equal to the size of the smallest unisexual family obtained without a solitary male in the count of a bisexual family, is extremely improbable.

The following is a list of the unisexual families obtained :—32♀♀, 47♀♀, 58♀♀, 61♀♀, 74♀♀, 77♀♀, 82♀♀, 85♀♀, 96♀♀.

The phenomenon of unisexual families was probably first demonstrated by Doncaster[7] in *Abraxas*. Since then it has been shown to occur in *Pediculus* sp. by Hindle,[10] in the Cecidomyidae by Barnes[1], and in the Mycetophilidae by Metz[14]. The last named worker has spent a number of years studying its cause in species of *Sciara*, in which females regularly occur which produce all male families and all female families.

Having eliminated the possibility of parthenogenesis, it was shown that the cause of unisexual progenies was not due to differential mortality in which all the male zygotes were eliminated from female-producing families and all the female zygotes from the male-producing families either early in their embryonic existence or later.

On the basis of genetical data which he accumulated, Metz came to the conclusion that sex determination in *Sciara* involves two distinct series of phenomena: (*a*) determination of the sex of the progeny as a whole; (*b*) determination of the sex of the individual.

Thus in one strain the male- and female-producing females are distinguishable by means of a mutant character, the gene for which appears to be completely linked with the differentiator responsible for "sex of progeny," and this suggested that the latter is determined by the zygotic constitution of the female, which presumably causes the elimination or inactivation of the kind of sperms responsible for the sex suppressed in the progeny. Moreover, this mutant character behaves in a typically Mendelian manner, and as female-producing females give female- and male-producing daughters in equal numbers, it is considered that the female-producing female is heterozygous for a pair of factors or chromosomes responsible for "sex of progeny," which may be written as follows :—

Female-producing females	Aa
Male- ,, ,, ...	aa
Male	aa

With regard to the "sex of the individual," a mutant character has been studied in *Sciara coprophila* which shows sex-linked inheritance of the kind expected when the female is XX and the male XY in sex chromosome constitution, and that the sex of the individual is held to be determined in the "ordinary way" by a pair of sex chromosomes in which the female is XX and the male XY. It should also be mentioned that not infrequently a few of the opposite sex occur in families otherwise unisexual, and they have been called "exceptional" males and "exceptional" females. The progeny of "exceptional" females from male families are all male-producers.

Although Metz has made a cytological study of *Sciara* spp., he has not yet found it possible to correlate his cytological and genetical data, and it seems improbable that a cytological study in *longispinus* would throw further light on the phenomenon of unisexual families.

(*c*) *The Fecundating Capacity of the Male.*

The bisexual families of *longispinus* produced the lowest proportion of males in any of the species examined, but despite this the fecundating capacity of its males are about the same as those of *citri*, the species with the highest proportion of males in its progeny.

The following figures give the number of females fertilised by twenty males of *longispinus* which had been separately supplied with a large number of virgin females in closed receptacles :—6, 4, 19, 0, 14, 12, 20, 0, 10, 12, 3, 11, 15, 1, 2, 0, 6, 9, 12, 8.

These figures give an average of 8·2 females per male, which, though not quite as great as the fecundating capacity of the male of *citri*, is more than sufficient to ensure the fertilisation of all the females in bisexual families.

The occurrence of unisexual families in this species introduces a complication, but if the data given in this paper are utilised and unisexual families are considered to occur in the proportion of one unisexual to two bisexual families and the maximum total progeny of any unisexual family is about 96 (the size of the largest unisexual family counted), then the average of 8·2 females per male would still be sufficient to ensure the fecundation of all the females from both kinds of families.

8. **Trionymus peregrinus,** Green.

Trionymus peregrinus occurs commonly on Amaryllidaceous plants, *e.g.*, *Amaryllis* spp., *Narcissus* spp., etc., in England, but there are no records of its occurrence abroad beyond the fact that Mr. Morrison informs me (*in litt.*) that it has been intercepted by the United States Plant Quarantine Department on *Nerine*, from a species of which genus it was originally described.

It is a typical *Trionymus*, that is to say, it combines the elongate form and root or base-of-stem feeding habit associated with most members of the genus that have those microscopic characters which have been indicated by Ferris[6] as the most likely to prove generic. Hence, although it probably is not so common as the species of *Pseudococcus* already examined, it was thought that this typical species might present characteristic features in connection with its reproductive activities. However, this did not prove to be the case, since reproduction was entirely non-parthenogenetic and the family sex ratios exhibited the fluctuating character associated with the genus *Pseudococcus*.

A species of *Amaryllis* proved a useful experimental host-plant and a few specimens of *Narcissus* sp. were also successfully employed.

Table XV summarises the results of the tests for parthenogenesis on ten *Amaryllis* plants.

TABLE XV.

Number of 3rd instar females on 4.ix.36	Virgin ♀♀ counted on 17.ix.36	Virgin ♀♀ counted on 30.ix.36	Virgin ♀♀ counted on 13.x.36	Virgin ♀♀ counted on 26.x.36	Virgin ♀♀ counted on 8.xi.36	Virgin ♀♀ counted on 22.xi.36	Virgin ♀♀ counted on 5.xii.36	Virgin ♀♀ counted on 18.xii.36
50	50	43	43	40	40	38	36	34
50	49	47	45	42	37	35	32	31
50	48	47	42	40	39	36	35	33
50	50	45	45	38	36	34	34	32
50	45	44	43	42	41	37	28	24
50	49	48	47	44	42	40	37	36
50	43	42	42	40	37	36	32	32
50	46	46	41	41	40	40	38	38
50	50	49	48	46	44	33	27	27
50	48	47	47	45	42	38	37	31
500	478	458	443	418	398	367	336	318

The preceding above table shows that out of 478 newly moulted virgin females on 17.ix.36, 318 were still living on 18.xii.36, 93 days later, when the experiment was terminated. Neither those which had died nor those still living had given any indication of reproductive activity. Nearly all those still alive showed the signs of extreme old age typical in the group, namely, the disintegration of the waxy pattern on the dorsal surface of the body and darkening of the body contents. The range of temperature recorded during the experiment varied from 21·34°C. to 26·71°C., with a mean temperature of 24·12°C. The relative humidity was constant at 100 per cent. throughout the experiment.

(*a*) *The Sex Ratio.*

The specific sex ratio of *T. peregrinus* was computed from the family sex ratios of twenty-four females. The series is set out in the following table.

TABLE XVI.

A Series of 24 Family Sex Ratios of Trionymus peregrinus, *Green.*

Family groups (according to number of progeny)	Number of female	Males	Females	Total progeny	Family sex ratios ♂♂ per 100 ♀♀	Maximum variation of sex ratios in each family group ♂♂ per 100 ♀♀
Families varying from 251–306	1	96	168	264	57·14+	
	2	70	188	258	37·23+	
	3	79	227	306	34·80+	
	4	64	208	272	30·77−	26·57−
Families varying from 201–250	5	72	129	201	55·81+	
	6	84	153	237	54·90+	
	7	62	170	232	36·47+	
	8	48	154	202	31·16+	
	9	47	165	212	28·48+	27·33+
Families varying from 151–200	10	64	129	193	49·61−	
	11	48	107	155	44·85+	
	12	50	139	189	35·97+	
	13	42	120	162	35·00+	14·61−
Families varying from 101–150	14	38	72	110	52·77+	
	15	38	72	110	52·77+	
	16	30	77	107	38·96+	
	17	32	84	116	38·09+	
	18	23	82	105	28·05−	
	19	13	88	101	14·77+	
	20	11	93	104	11·83−	41·94−
Families varying from 51–100	21	25	70	95	25·71+	
	22	13	41	54	31·70+	
	23	20	77	97	25·97+	
	24	13	51	64	25·49+	10·22+
Totals ...	—	1,082	2,864	3,946		

The specific sex ratio = the mean of the family ratios

$$= \bar{x} = \frac{T}{n} = \frac{888 \cdot 0}{24}$$

= 37·01 ♂♂ per 100 ♀♀

The sum of the squares of the deviation from the mean = 36328·5388

The standard error $= s = \sqrt{\frac{U}{n\,(n\text{-}l)}} = \sqrt{\frac{3450{\cdot}3358}{552}} = \sqrt{62{\cdot}506}$
$= 7{\cdot}906$

∴ the specific sex ratio of *T. peregrinus* = 37·01 ± 7·906.

The maximum total progeny produced by any female was 306 and the minimum was 54. The average number of progeny per female was 164·42—. The range of temperature recorded during the experiment varied from 19·98°C. to 25·34°C., with a mean of 23·54°C. The relative humidity as in the other experiments was maintained at 100 per cent.

9. Discussion.

A perusal of the somewhat extensive literature which has accumulated on this important group, the PSEUDOCOCCINAE, cannot fail to give the impression that parthenogenesis is the rule rather than the exception and that what really requires demonstration is the occurrence of sexual reproduction. My examination of five of the commoner species, however, has failed to demonstrate the occurrence of either the haploid or the diploid type of parthenogenesis, nor did it prove possible for mature females when denied fertilisation for long periods to become facultatively parthenogenetic. Hence, species of *Pseudococcus* should not be regarded as parthenogenetic, no matter how impressive the *prima facie* evidence appears to be, unless the fact has been experimentally demonstrated.

Associated with and largely responsible for the misconception about parthenogenesis in mealy-bugs is the apparent scarcity of males. It is shown that the relative numbers of the sexes varies greatly from species to species ; in *citri* the sexes occur in approximately equal numbers, whereas in *longispinus* the ratio of males to females is about 1 : 5, and where unisexual families of females are numerous the specific sex ratio must be even wider. The species *gahani*, *maritimus* and *peregrinus* occupy intermediate positions ; the specific sex ratios of *gahani* and *maritimus* are in the neighbourhood of one male to two females, whilst the ratio prevailing in *peregrinus* approximates more nearly to one male to three females.

Since it has been shown that it is possible for single males of both *citri* and *longispinus* to fertilise about twenty females, it seems to be improbable, even in the case of *longispinus*, that species of *Pseudococcus* are ever seriously restricted in numbers through lack of males. Moreover, the experiments on delayed fertilisation in *citri* suggest that a scarcity of males in one generation will result in an automatic increase in the number of that sex in the next.

An examination of the five series of family sex ratios from which the specific sex ratios have been computed reveals considerable intra-specific variability in the family ratios. Thus the series of family sex ratios of *citri* vary from 82·75 to 128·38 ♂♂ per 100 ♀♀ ; those of *gahani* vary from 15·15 to 97·53 ♂♂ per 100 ♀♀ ; those of *maritimus* vary from 8·69 to 377·77 ♂♂ per 100 ♀♀ ; those of *longispinus* vary from 9·74 to 55·55 ♂♂ per 100 ♀♀ ; and those of *peregrinus* vary from 11·83 to 57·14 ♂♂ per 100 ♀♀.

A comparison of the sex ratios of the largest families in each species shows that wide variations may occur in them and this suggests that the variability of the family sex ratios is mainly the reflection of variable primary ratios. For instance, consider the series of 47 family ratios recorded for the species *citri* ; the average number of progeny per female works out at 238·57 ♂♂ per 100 ♀♀, but the total progeny of only twelve exceed 300 and of these only four approach or slightly exceed 400. Thus, in *citri*, the progeny of only one female in four exceeds 300 and only one in twelve reaches the neighbourhood of 400, and it may be taken as virtually certain that most females which produce over 300 offspring approach close to their reproduction maxima, and therefore in these large families differential sex mortality from whatever cause can be disregarded as a significant factor, and it follows that substantial divergences in the sex ratios of such families can be interpreted only as divergences in the ratios at the time of sex determination.

A comparison of the sex ratios of the twelve females of *citri* whose families exceeded 300, grouped according to size, will illustrate the point.

Family group number	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of sex ratio in family group ♂♂ per 100 ♀♀
1	166	140	306	118·57—	20·50—
1	153	156	309	98·07+	
2	172	150	322	114·66+	21·85+
2	155	167	322	92·81—	
3	170	184	354	92·39—	5·86+
3	178	185	363	96·21+	
3	169	172	341	98·25+	
4	190	214	404	88·75+	19·10+
4	204	194	398	105·15—	
4	206	191	397	107·85—	
4	193	184	377	104·89—	
4	196	188	384	104·25+	

By a comparison only of the sex ratios of families which exceeded 300 I do not wish to imply that the females of lower fecundity did not in many cases attain or approach their potential maxima ; all that is implied is that in the case of the females of much lower maxima the possibility of differential loss cannot be completely excluded, and in addition differences of a percentage character are of less significance. Nevertheless it is maintained in their cases also that the principal cause of variability in the family sex ratios, as experimentally determined, is variability in their primary sex ratios.

This variability in the family sex ratios of *citri* is also exhibited in those derived from females whose fertilisation had been delayed. The sex ratios of 36 females, where fertilisation had been delayed for six weeks, varied from 114·60+ to 244·44— ♂♂ per 100 ♀♀, but only five families exceeded 300, and their sex ratios are compared in two groups as follows :—

Family group number	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of sex ratios in each family group ♂♂ per 100 ♀♀
1	228	163	391	139·87+	19·53+
1	207	172	379	120·34+	
2	218	109	327	200·00+	64·45+
2	185	117	302	158·11+	
2	183	135	318	135·55+	

In the case of fifteen females whose fertilisation was delayed for 56 days, two families only exceeded 300 in number, and although the difference in the sex ratios was as much as 20 per cent., the two families also varied in size to the extent of 52 individuals and the variation in the sex ratio is perhaps not fully significant.

Family group number	Males	Females	Total progeny	Family sex ratio per 100	Maximum variation of sex ratios in each family group ♂♂ per 100 ♀♀
1	270	84	354	321·98−	
1	305	101	406	301·98−	20·00−

An examination of the series of family sex ratios pertaining to the species *gahani* shows an even greater variability than those of *citri*. The average number of progeny per female is 198·18, but only 9 females out of a total of 61 are responsible for families exceeding 300 in number and only 3 approach or slightly exceed 400. Hence, only 1 female in every 6·99 exceeds 300, and only 1 in 20·30 reaches the neighbourhood of 400, so that in this species also it appears that the potential maximum for the most prolific females is about 400.

The sex ratios of the nine largest families of *gahani* are compared in the following list.

Family group number	Males	Females	Total progeny	Family sex ratio per 100	Maximum variation of sex ratio in each family group per 100
1	117	199	316	58·79−	
1	133	204	337	65·19+	
1	102	245	347	41·63−	23·56−
2	134	234	368	57·26−	
2	100	273	373	36·63−	
2	104	270	374	38·51+	20·63−
3	168	230	398	73·04+	
3	171	234	405	73·07+	
3	82	324	406	25·30+	47·77+

In order to illustrate the significance of the differences between the sex ratios of the families in group 3, it may be pointed out that it would require a family of 561, produced by the addition of 155 males to the family with a sex ratio of 25·30+, in order that the latter should be converted into a ratio of 73·04+♂♂ per 100 ♀♀. A family of 561 is far beyond the reproductive range of individual females of any of the species of *Pseudococcus* examined, and therefore the widely differing sex ratios shown above cannot be accounted for by a differential sex mortality.

In the species *longispinus* also, 400 appears to be near the potential maximum for any female of the species, and yet we find a variation of nearly 10 ♂♂ per 100 ♀♀ in families which approach this figure, as the following comparisons show.

Number of family group	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of the sex ratio in the family group ♂♂ per 100 ♀♀
1	71	327	398	21·71−	
1	50	320	370	15·62−	
1	42	348	390	12·06+	9·65−

In the species *maritimus* also, a comparison of the sex ratios of three of the largest families show wide diviergences.

Number of family group	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of the sex ratio in the family group ♂♂ per 100 ♀♀
1	79	152	231	51·97+	
1	67	141	208	47·51+	
1	48	184	232	26·08+	25·89+

Similarly, in the species *peregrinus* the same state of affairs is to be found in a comparison of the sex ratios of four of the largest families in the series belonging to that species.

Number of family group	Males	Females	Total progeny	Family sex ratio ♂♂ per 100 ♀♀	Maximum variation of the sex ratio in the family group ♂♂ per 100 ♀♀
1	96	168	264	57·14+	
1	70	188	258	37·23+	
1	79	227	306	34·80+	
1	64	208	272	30·77−	26·57−

A study of family sex ratios of species of *Pseudococcus* suggests that whilst the series for each species lies for the most part in a characteristic zone, very wide variations frequently occur in the ratios of females of the same species, even when their families are in the neighbourhood of the maximum size for their species.

With regard to the operation of a sex-determining mechanism in animals in general, the most important established fact is that one sex always produces two sorts of gametes, one kind male-producing, the other kind female-producing, and that if these are produced in equal numbers and are of equal functional efficiency, equal numbers of males and females should be produced.

The study of sex ratios is in large part an investigation of the causes which produce divergences from this parity ratio, which the digametic nature of the gametes of one of the sexes tends to bring about.

In an examination of the known disturbing causes of primary sex ratios which may conceivably cause the characteristic fluctuations in the sex ratios of *Pseudococcus*, it may be pointed out that, though unbalanced lethal sex factors may play a part in producing some of the variability in the sex ratios of the smaller families, the fluctuations are of too general a nature to be even partly accounted for by this factor. Since lethal factors can only affect the sex ratio by producing non-viable zygotes which are all of one sex and which are thus responsible for a differential loss of the sexes, their influence on the variability of the sex ratios of the largest families can only be slight.

A much more effective agent in producing intra-specific variations of the primary ratio would be the occurrence in *Pseudococcus* of the type of inter-sexuality which occurs in the progeny of the inter-racial crosses of *Lymantria*.[8] This would be indicative of the fact that the pair of opposed factors or sets of factors responsible for sex in *Pseudococcus* are frequently within the range of genic balance, and that small fluctuations of the valencies of the sex factors from female to female would be productive of variability in their sex ratios.

A large number of sections of the gonads of both sexes of *citri* and *maritimus* were scrutinised for indications of intersexuality, but none was detected. Moreover, it seems likely that, owing to the extreme form of sexual dimorphism prevalent in *Pseudococcus*, the occurrence of varying grades of intersexes would result in the production of forms of a nature so bizarre that some of them could not fail to escape detection.

The absence of intersexuality is also important, because it favours the possibility that sex in *Pseudococcus* is early and decisively established, and this tends to diminish the probability that environmental factors have played an important part in sex determination. The temperature ranges in which the series of sex ratios were determined were all very narrow, and the progeny of the females of each species were reared on the same kind of food-plant with the exception of *peregrinus*, for which a few specimens of a species of *Narcissus* were used in addition to *Amaryllis*.

Lighting conditions were the same for all the females in any experiment, and the relative humidity was constant throughout.

A cytological search for the cause of the variable sex ratios immediately attracts attention to the possibility of a variable differential production of one kind of gamete from the digametic sex, which happens to be the male in *Pseudococcus*.

The spermatids are double, containing one of each kind of spermatozoon, and no degeneration could be detected in any of a large number of spermatids examined in the species *citri* and *maritimus* ; thus it seems that a variable differential production of gametes must be eliminated as a possibility. Whether, however, the imperfect and relatively late formation of the spindle fibres at one of the poles in the reduction division is indicative of an incipient degeneracy in one kind of spermatozoon, which is not evident morphologically, but which is expressed in a variable vitality that causes a corresponding variability in its functional efficiency, seems to be the only visible explanation of the variability in the primary sex ratios of large families in *Pseudococcus*.

10. Summary.

1. The male of *Pseudococcus* is co-equal in importance with the female for the propagation of the species. Virgin females of *P. citri*, Risso (both aerial and root forms), *P. maritimus*, Ehr., *P. gahani*, Green, *P. longispinus*, Targ., and *T. peregrinus*, Green, are incapable of producing offspring. No form of parthenogenesis occurs in these five species. Only fertilised eggs develop.

2. The relative abundance of the male sex varies greatly from species to species. The specific sex ratio of *citri* is 101·62± 1·54 ♂♂ per 100 ♀♀, estimated from 11,413 progeny from 47 females ; that of *maritimus* is 59·65± 9·39 ♂♂ per 100 ♀♀, estimated from 4,630 progeny from 42 females ; that of *gahani* is 43·025± 2·28 ♂♂ per 100 ♀♀, estimated from 12,092 progeny from 61 females ; that of *longispinus* (for bisexual families only) is 19·28± 2·27 ♂♂ per 100 ♀♀, estimated from 4,084 progeny from 19 females ; and that of *peregrinus* 37·01± 7·906 ♂♂ per 100 ♀♀, estimated from 3,946 progeny from 24 females.

3. The fecundity of the females of *citri* varies from 38 to 404, with an average family per female of 238·57+ ; the fecundity of females of *maritimus* varies from 8 to 189 with an average family per female of 110·23+ ; the fecundity of females of *longispinus* varies from 32 to 398, with an average family (bisexual) per female of 214·95— ; the fecundity of females of *gahani* varies from 57 to 406, with an average family per female of 198·20— ; the fecundity of females of *peregrinus* varies from 54 to 306, with an average family per female of 164·41+.

4. The family sex ratios of *Pseudococcus* show great intra-specific variability in families from females of both low and high fecundity under uniform conditions of food and environment.

The family sex ratios of *citri* vary from 82·75 to 128·38 ♂♂ per 100 ♀♀; the family sex ratios of *maritimus* vary from 8·69 to 377·77 ♂♂ per 100 ♀♀; the family sex ratios of *gahani* vary from 15·15 to 97·53 ♂♂ per 100 ♀♀; the family sex ratios of *longispinus* vary from 9·74 to 55·55 ♂♂ per 100 ♀♀; and the family sex ratio of *peregrinus* vary from 11·83 to 57·14 ♂♂ per 100 ♀♀.

The fact that great divergences may occur in the sex ratios of large families which are in the neighbourhood of the potential maximum for their species, as well as in smaller families proves that these divergencies are the result of very variable sex ratios at the time of sex determination, because in the largest families differential sex mortality is eliminated as a significant factor.

5. The cause of the intra-specific variability of the family sex ratios was sought. The following facts were ascertained in the species *citri* and *maritimus*:—

(*a*) There is no differential production of gametes in the digametic sex. The spermatids are double, containing a fully formed spermatozoon of each kind. Hence the two kinds of spermotozoa are produced in equal numbers and the variability of the sex ratios cannot be explained by a variable differential production of gametes.

(*b*) There is no intersexuality. This disposes of the possibility that the balance of the valencies of the opposed factors for sex is in the region of genic balance with the consequence that relatively small fluctuations in their valencies from individual to individual would produce significant variations in their sex ratios.

Importance is attached to an abnormality in the reduction division of the male. In the male the chromosomes can be distinguished into two groups of five. In one group the chromosomes are massed close together and appear to act together in many respects like a unit; the other five chromosomes may be called in contradistinction the loose group. Random segregation does not occur at reduction and the massed group invariably goes to one pole and the loose group to the other. The spindle fibres attached to the loose group are always late in appearing and are imperfectly formed and the chromosomes of this group exhibit a lack of co-ordination in travelling to their pole.

It is suggested that this imperfection in the spindle fibres of the loose group of chromosomes may be indicative of an incipient degeneracy in one set of gametes which is not evident in the fully formed sperms but which is expressed in a variable vitality that causes a variability in their functional efficiency.

This explanation would account for the variability of both the specific and the family sex ratios of *Pseudococcus*.

6. The phenomenon of unisexual families occurs in *Pseudococcus*. Unisexual families of females were obtained from fertilised females in the species *longispinus*.

7. Delayed fertilisation in *citri* results in an increased proportion of males in the sex ratios. The increase of males is proportional to the period of delay before fertilisation.

The mean of the family sex ratios of 36 females whose fertilisation was delayed for six weeks was 180·89 ± 6·20♂♂ per 100♀♀ as compared with 101·62 ± 1·54♂♂ per 100♀♀, the normal specific sex ratio of *citri*; the mean of the sex ratios of 15 females when the delay was eight weeks was 327·40 ± 11·63♂♂ per 100♀♀; and the mean of the sex ratios of ten females after a delay of ten weeks was 991·091 ± 460·50♂♂ per 100♀♀.

8. Of the five species whose specific sex ratios were determined *citri* has the highest and *longispinus* the lowest ratio. The fecundating capacity of the males in these two species was tested and compared. The highest number of females fertilised by a single male of *citri* was 23, and 13 males produced an average of 9·07 females. The highest number of females fertilised by a single male of *longispinus* was 20, and 20 males produced an average of 8·2 females. Hence even in *longispinus* there always appear to be ample males to fertilise the females.

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A NEW SPECIES OF *APANTELES* (HYM. BRAC.) BRED FROM *MYELOIS CERATONIAE* ATTACKING CAROBS IN CYPRUS.

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Apanteles myeloenta, sp. n.

♀. Black; the front femora in the apical half or third, the front tibiae and tarsi (save for the black feet), middle femora in about the apical fifth or sixth, middle tibiae (save commonly for some darkening in the apical two-thirds above), middle tarsi (save for the feet and last joint, which are black), and the hind tibiae in about the apical fifth or sixth, red testaceous; tegulae testaceous; palpi pale; tibial spurs white; wings hyaline, the setae apparently coloured; the costal veins in the basal half more or less colourless, as are all the wing-veins; costal veins apically, and the borders of the stigma, light brown or brown, the metacarp brown or dark brown; stigma otherwise hyaline.

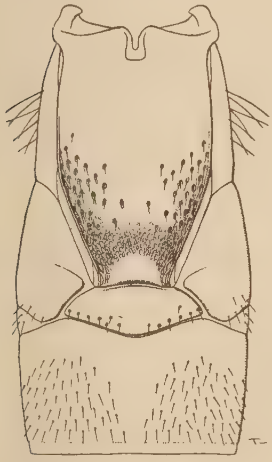
Fig. 1. *A. myeloenta*, sp. n., basal tergites, ♀ (× 54).

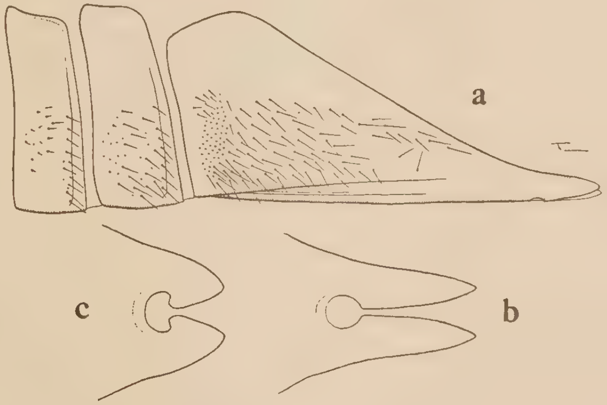

Fig. 2. (*a*) *A. myeloenta*, sp. n., apical ventrites, side view, ♀ (× 40); (*b*) *A. myeloenta*, sp. n., (*c*) *A. cajani*, Wilkn., apex of hypopygium, opened out, dorsal view, ♀, to show shape and relative size and position of foramen (× 80).

♂. Black; front femora in the apical third, front tibiae and tarsi (save for the black feet), middle femora at extreme apex, middle tibiae basally, middle tarsi (save for the feet and the last joint, which are black), and hind tibiae in the basal sixth, red testaceous; tegulae testaceous; palpi pale; tibial spurs white; wings white hyaline, the setae white; costal and all wing-veins colourless, white; the borders of the stigma opaque, perhaps to some extent coloured above; metacarp dark brown, sometimes even almost black; stigma otherwise hyaline.

♀♂. *Head*: clypeus and face throughout punctate (degree 3); facial depressions noticeably nearer to apex of clypeus than to the eyes; frontal orbits, frons, and vertex, throughout minutely punctate (degree 2); posterior ocelli equidistant from each other and the eyes, or rather nearer to the eyes; flagellum of ♀ shorter than the combined length of the thorax and abdomen, about equal to twice the length of the thorax, of ♂ longer than the combined length of thorax and abdomen together with twice the length of the head. *Thorax*: mesonotum more or less dull, throughout with very closely placed, often contiguous punctation (degree 3–4), which gives the effect of minute rugosity until examined closely, the lines of the notauli definitely minutely rugose; immediately in front of, and touching, the scutellar sulcus, and occupying about the medial half of the breadth of the mesonotum at this point, is a small transverse area that is highly shining and entirely smooth save for some half-dozen exceedingly minute punctures (degree 1); scutellar sulcus bisinuate; disc of scutellum with closely placed, often contiguous punctation (degree 3–4) broadly down the lateral margins, otherwise minutely punctate (degree 1) and much more shining than the mesonotum; the non-excavate area of the lateral faces of the scutellum clearly reaching up beyond half-way to base of scutellum; propodeon with a median longitudinal carina which in the basal fourth is commonly obsolete to wanting, but which in the apical portions is strongly marked, and which in the apical half is widened or bifurcated so as to form a large, smooth, flat, triangular, apical area; this carina emits on each side short, somewhat oblique, rugose carination; propodeon otherwise, in basal half punctate (degree 3), in apical half largely entirely smooth and shining save for some strong rugosity broadly down the lateral margins. *Wings*: the 1st abscissa of the radial considerably longer than and slightly angled with the transverse cubital; upper portion of basal vein long, longer than the pigmented portion of the 2nd abscissa of the cubital. *Legs*: hind coxae above in about the basal half closely coarsely aciculately punctate, or even finely rugose, above in about the apical third longitudinally aciculate, on outer faces minutely punctate (degree 2); the longer hind tibial spur half, and the shorter spur in the ♂ about one-third and in the ♀ rather less than one-third, the length of the basal joint of the hind tarsus. *Abdomen* (figs. 1–3): 1st tergite in ♀ in about the basal half strongly excavated, highly shining, and entirely smooth, in about the apical half strongly turned over and with well marked, well separated punctation (degrees 3–4 and 4) broadly down the lateral margins, apically with much aciculation which delimitates a large area that occupies the whole of the extreme apex and is highly shining and entirely smooth, in ♂ much as in ♀ save that the apical half is not so strongly turned over, that the punctation is almost invariably much weaker (degree 3) and does not extend so far down towards the apex, and that the apical aciculation is invariably entirely wanting; 2nd tergite in ♀ irregularly punctate (degree 3–4) transversely across in about the apical third, otherwise entirely smooth, in ♂ as in ♀ save that the punctures are much weaker (degrees 2 and 3); 2nd suture well marked, bisinuate, always strongly bisinuate in ♀ but not always strongly so in ♂; 3rd tergite entirely smooth broadly across base, narrowly across apex, and down the middle, otherwise with very regularly placed, minute punctation; succeeding tergites minutely punctate; majority of ventrites of ♀ with

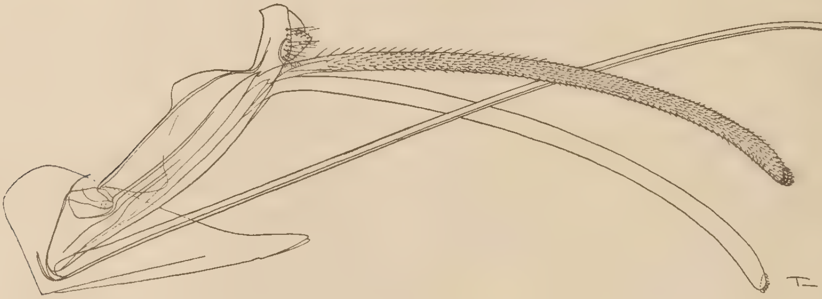

Fig. 3. *A. myeloenta*, sp. n., genitalia, ♀ (× 27).

median longitudinal suture ; ovipositor and sheaths elongate, the sheaths longer than the combined length of hind tibia and tarsus, the ovipositor about as long as combined length of trochanter, trochantine, femur, tibia, and tarsus of hind leg ; hypopygium membranously acute.

Length : ♀, 3·5 mm. ; ♂, 3·0 mm.

Described from the following material :—IMPERIAL INSTITUTE OF ENTOMOLOGY : Cyprus, Kyrenia, 1 ♀, 18.viii.1935, 1 ♀, 23.viii.1935, 1 ♂, 11.vii.1935, 1 ♂, 7.x.1935 (*C. Papachrysostomou*), Kyrenia Pass, 3 ♀♀, 24.vii.1935, 26.vii.1935, 2.x.1935 (*C. Papachrysostomou*), Kyrenia, 18 ♀♀ (one the *type*), 13 ♂♂, 1936 (*H. M. Morris*).

Type deposited in the British Museum.

Host. This new species is recorded as a parasite of the Pyralid *Myelois ceratoniae*, Zell., a pest of the beans of the carob-tree, *Ceratonia siliqua.* Mr. Morris records further, in a letter to the present writer, that this parasite has so far only been bred from material in old carob-pods on the trees in the autumn.

Cocoons unknown.

The species that I am here putting forward as new can be made to agree neither with any of the palaearctic species included by Marshall in his monograph, by far the greater majority of the types of which are known to me, nor with the descriptions of any of the palaearctic species published subsequently to Marshall's works, the majority of which latter species are also known to me. In Marshall's key my new species runs to *lacteus* and *xanthostigmus*, which are quite distinct. As far as the American species are concerned, *myeloenta* will agree with none of the many that are represented in the British Museum ; and in Muesebeck's key (1920) it runs fairly easily, and certainly nowhere else than, to *etiellae*, Vier., which is represented in the British Museum by authentically determined material, and which is quite distinct on account of the length of the ovipositor. In my own key (1932, Trans. Ent. Soc. London **80**) *myeloenta* runs directly to *cajani*, Wilkn., in couplet 99. My new species and *cajani* are, in fact, remarkably similar, but may easily be separated by the characters I give in the revised couplet, below :—

99. Ovipositor sheaths very considerably longer than hind tarsus..............99a.
Ovipositor sheaths definitely shorter than hind tarsus..................... 100.

99a. Mesonotum with strong, close but separated, punctation (degrees 4 and 5) ; hypopygium with a preapical foramen which is twice its own longitudinal diameter from apex (fig. 2*c*) ; India..............................*cajani*, Wilkn.

Mesonotum with very closely placed, often contiguous, punctation (degree 3–4) ; hypopygium with a preapical foramen which is three times its own longitudinal diameter from apex (fig. 2*b*) ; Cyprus .... *myeloenta*, Wilkn.

I am taking this opportunity, also, to add to my key two American species that have lately become known to me, which belong to this group of the genus and have a median longitudinal carina, and of which authentic material has lately come into the possession of the British Museum, from the United States National Museum, through our policy of exchange. Couplets 96 and 97 of my key, therefore, are to be altered, as below :—

96. Hind coxae of ♀ in greater part or wholly red testaceous .... 96a.
Hind coxae black...97.

96a. Mesonotum and disc of scutellum of ♀ red testaceous ; propodeon entirely smooth (save for longitudinal carina) and highly shining ; Br. Guiana......... *ruficollis*, Cam.

Mesonotum and disc of scutellum of ♀ black ; propodeon finely rugose and more or less dull...96b.

96b. Abdomen with 2nd, 3rd, and perhaps 4th tergites, and ovipositor sheaths, red testaceous ; U.S.A. .... *cinctiformis*, Vier.

Abdomen with tergites and ovipositor sheahts black ; U.S.A. *papaipemae*, Mues.

97. Propodeon coarsely rugose and dull ; Grenada, St. Vincent ... *aciculatus*, Ashm.

Propodeon entirely smooth and highly shining, save perhaps for some sculpture in neighbourhood of median longitudinal carina and of lateral and apical margins ; U.S.A. .... *sesiae*, Vier.

NEW INJURIOUS CURCULIONIDAE (COL.).

By Sir Guy A. K. Marshall.

(Plate XII).

The types of the following new species have all been deposited in the British Museum.

Subfamily Brachyderinae.

Blosyrus ipomoeae, sp. n. (Plate XII, fig. 1).

♂. Derm black, with dense brown scaling; prothorax with an indefinite paler patch in a line with interval 3 of the elytra and extending from the base to the middle; elytra with variable black patches on intervals 3 and 5 and the usual ill-defined oblique paler band from the middle of interval 3 to the shoulder.

Head with three deep sulci, the outer ones curved and shallower than the median one; the median frontal areas widely separated behind and there scarcely narrower than in front, the outer areas becoming higher laterally but not overhanging the eyes, which are prominent and highest behind the middle. *Rostrum* transverse, parallel-sided, the basal incision very deep, the genae not projecting; the dorsum with a large median impression containing a bare carina that bifurcates in front and a very shallow oblique sulcus on each side; the hind margin of the epistome sharply carinate. *Antennae* with joint 1 of the funicle as long as 2 + 3, 3–6 moniliform, somewhat transverse and subequal, 7 longer and broader. *Prothorax* transverse (3 : 4), strongly rounded laterally in the anterior half, widest at one-third from the apex, rapidly narrowing behind but not constricted, and without any apical constriction; the gular margin sinuate, but not angulate laterally; the dorsum convex longitudinally, highest beyond the middle, deeply rugose, without any median carina; the setae on the disk short, stout, brown and suberect. *Elytra* subglobose, somewhat longer than broad (6 : 5), subtruncate at the base, which is not constricted, the sides gently curved from the obtuse basal angle to the humeral tubercle on interval 7, there being a similar tubercle immediately below it on interval 9; the posterior declivity quite perpendicular close to the apex; the sulci with deep round punctures which are partly filled with scaling and scarcely diminish behind; interval 1 flattened, the others convex, 3, 5 and 7 being strongly elevated but without any tufts or tubercles except the humeral one, the numerous irregular setae being short stout and subrecumbent. *Legs* with pale brown scaling, the posterior pairs of femora with a paler band beyond the middle and a dark area below it; the tibiae with a broad dark band on the apical half. *Venter* of ♂ with the terminal ventrite flattened in the middle.

Length 6·5–7·0 mm., breadth 4·5–5·0 mm.

S. Rhodesia: Salisbury, 2 ♂♂, 9.iv.1937 (*A. Cuthbertson*).

Reported as a pest of sweet potatoes, the adults eating the leaves.

Most nearly related to *B. fasciculosus*, Pér., which is common in the same locality and differs in having a marked angular projection on each side of the gular emargination of the prosternum; the elytra also have an obtuse tubercle near the base on intervals 3 and 5, and fasciculate tubercles posteriorly, and the sides are quite straight from the basal angle to the humeral tubercle.

Analeurops, gen. n.*

Head broad, not constricted behind the eyes, continuous with the rostrum, the base of which is somewhat broader than the forehead ; eyes almost flat. *Rostrum* subconical, much narrowed in front, with the sides vertical and the genae not visible from above ; epistome very small, obtusely marginate ; mandibles squamose, multisetose, with a strong median tooth ; mentum slightly sunk in the buccal cavity, with numerous setae ; scrobes narrow, parallel-sided, passing well below the eyes. *Antennae* with the scape slender, abruptly clavate and reaching to about the middle of the eye ; funicle not squamose, joint 1 longer than 2 + 3. *Prothorax* transverse, arcuate and marginate at the base, without vibrissae. *Elytra* fitting closely to the prothorax, without humeral calli, with the lateral margins strongly inflexed and with ten complete striae. *Sternum* with the gular margin deeply sinuate, the coxae in the middle of the prosternum, and the intercoxal sclerite not tubercular ; mesepimeron long and narrow, separating the mesepisternum from the base of the elytron ; metasternum much shorter than the middle coxae, without any transverse fold in front of the hind coxae, the metepisterna narrowing rapidly behind and the suture complete. *Venter* with the intercoxal process ogival, much narrower than a hind coxa ; ventrite 2 longer than 3 or 4. *Legs* short ; femora simple ; the front tibiae with the external apical angle produced outwardly into a broad pointed process ; the corbels of the hind tibiae broadly enclosed, not ascending the tibiae, their dorsal edge being as long as the apical one, the bevel squamose, but the inside of the corbel bare ; claws small, connate.

Genotype : *Analeurops cuthbertsoni*, sp. n.

Nearly allied to the South African *Leurops*, Mshl. 1919, which differs in having the front tibiae with the external apical angle rounded ; the hind corbels are squamose internally and ascend the tibia, their dorsal edge being longer than the apical ; and the scrobes are widened behind.

Analeurops cuthbertsoni, sp. n. (Plate XII, fig. 2).

♀. Derm black, with dense variegated scaling ; head and rostrum with grey or light brown scaling and a paler patch above each eye ; prothorax with a broad median dark brown stripe, on each side of it a narrower pale brown one, then a broader one of principally grey scales, and finally a well-defined dark stripe on the pleurae just below the dorsal margin (the dorsal stripes usually ill-defined and sometimes almost obliterated) ; elytra light brown with very variable paler and dark patches ; in well marked specimens there is a macular dark brown stripe on intervals 5 or 6, and in one specimen almost the whole dorsal area is dark brown as far as stria 6 ; underside with uniform sparser grey scaling.

Head with shallow confluent punctures hidden by dense scaling ; a small median fovea extending backwards as a short stria. *Rostrum* (with mandibles) about as long as its basal width, which is twice the apical width, with the sides straight ; the dorsum flat, with a shallow median impression on the apical half containing a low fine carina. *Prothorax* rounded laterally, widest at about one-third from the base, where there is a small laterally projecting spine (sometimes broken off), narrowly constricted at the apex, the basal angles entirely rounded off ; the dorsum convex longitudinally, with very shallow small dense confluent punctures and often minute granules between them, but all hidden by scaling, and with an abbreviated narrow smooth median line, sometimes shallowly striate ; the short scale-like setae recumbent on the disk and suberect laterally. *Elytra* broadly oblong-ovate, almost parallel-sided in the middle, broadly rounded behind, jointly sinuate at the base, with the basal angles produced forwards in a small tubercular projection, embracing the base of the prothorax ; the dorsum even, with shallow striae, the punctures in which are partly visible through the scales; the intervals broad, almost flat, with a row of dark spatulate recumbent setae, which are only conspicuous on the declivity, where they are mostly whitish. *Legs* red-brown, with rather sparse greyish scaling.

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* Erroneously printed as *Analeucops* on Plate XII.

Length 3·5–5·2 mm., breadth 2–3 mm.

S. RHODESIA: Salisbury, 6 ♀♀, 30.xi.1936 (*T. C. Pascoe*—type); Hartley, 6 ♀♀, 17.xii.1929.

Mr. A. Cuthbertson, Department of Agriculture, S. Rhodesia, reports that this species is a pest of young tobacco plants near Salisbury; the Hartley specimens were attacking young cowpeas and sunn hemp.

Naupactus bondari, sp. n.

♂♀. Derm black, with sparse narrow metallic green scales and some ill-defined green stripes; prothorax with an indefinite curved stripe on each side formed of broader and rather paler green scales; elytra with the following ill-defined markings of broad green scales: a transverse band or patch across the base, a stripe on interval 5 starting before the middle and extending almost or quite to the apex, and frequently a stripe on interval 7 from behind the shoulder to beyond the middle; front legs black with the tibiae rarely reddish, the hind pairs red with the tarsi infuscated (rarely red).

Head with the punctures separated by more than their own width and a deep frontal sulcus, the scales narrow and sparse, the eyes semicircular. *Rostrum* longer than broad, impressed in the middle, with a deep median sulcus on the basal half continuous with that on the head, sparsely punctate and with the scales broader than those on the head. *Antennae* testaceous, the scape reaching the front margin of the prothorax. *Prothorax* transverse, strongly rounded laterally in ♂, less so in ♀, widest at about the middle, bisinuate and carinate at the base, shallowly constricted at the apex; the dorsum longitudinally convex in ♂, almost flat in ♀, with low subconfluent granules in ♂, more granulato-punctate in ♀, with a more or less abbreviated fine median stria which is often obsolete; scales very narrow on the disk, those in the lateral stripes broad. *Elytra* narrowly elongate in ♂, much broader in ♀, separately rounded at the base, with the basal margin slightly raised; the shallow striae containing strong separated punctures; the intervals rugulose and more or less wrinkled transversely on the basal half, about as wide as the striae in ♂, much wider in ♀; the sparse green scales mostly narrow, those in the denser stripes and patches much broader; the numerous short dark subrecumbent setae inconspicuous, but becoming long, slender and erect close to the apex. *Legs* with fine recumbent setae which are green on the black front femora and pale elsewhere; ♂ with a single small tubercle on the front coxae (sometimes present also in ♀), the front tibiae only moderately incurved at the apex and with a single row of fine denticles on the lower edge. *Aedeagus* of ♂ (fig. 1, *a*) with the lamina forming about half the length of the organ and quite flat, parallel-sided and not turned up at the apex, which is broadly and regularly rounded, without any lateral constriction.

Length, ♂ 7–9 mm., ♀ 9·0–10·5 mm.; breadth, ♂ 2·5–3·5 mm., ♀ 4·0–4·7 mm.

BRAZIL: Bahia, 3 ♂♂ 2 ♀♀ (coll. Fry); Bahia, 2 ♂♂ 2 ♀♀, on cacao, 1936 (*Dr. G. Bondar*).

Closely allied to *N. bipes* and *pithecius*, Germ. 1824, but much smaller.

N. bipes differs in both sexes in having the prothorax much more strongly rounded laterally and much more convex longitudinally; the elytra are more elevated at the base, and the scales on the middle of the disk are scarcely smaller than those at the sides; the front tibiae are much more strongly curved inwards at the apex, especially in the ♂, in which sex they are armed with a double row of much coarser teeth and the front coxae bear two tubercles ; the aedeagus (fig. 1, *b*) is also very different, the lamina being slightly sinuate laterally in the middle and rather abruptly narrowed at the apex, which is narrowly subtruncate and slightly up-turned.

N. pithecius more nearly resembles *bondari* in the form of the prothorax and front tibiae, but the legs are all black ; the elytra are much narrower and more elongate (especially in the ♀) and more strongly wrinkled transversely, so that the striae are rather indistinct and the discal scales are not narrow ; the lamina of the aedeagus (fig. 1, *c*) is curved upwards from about its middle and deeply sinuate on each side close to the apex, which is dilated and broadly truncate.

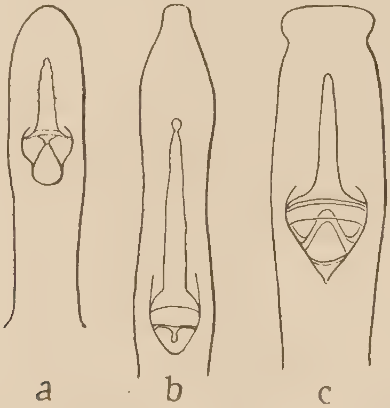


Fig. 1. Terminal portion of male aedeagus of : (*a*) *Naupactus bondari*, Mshl., sp. n. ; (*b*) *N. bipes*, Germ. ; (*c*) *N. pithecius*, Germ.

Subfamily Eremninae.

Eremnus angustirostris, sp. n.

♂♀. Derm red-brown to piceous, with dense uniform bright green scaling above, the underside grey.

Head with very shallow confluent punctation (entirely concealed by scaling) and a few erect setae ; forehead convex, the median fovea minute. *Rostrum* slender, about as long as the pronotum, narrowing from the base to the middle and then widening to the apex, laterally compressed so that the median dorsal area is much narrower than usual, the space between the antennae being only a little wider than the adjoining scrobes, the dorsal area rounded off laterally in the basal half, without any lateral edges and without a median stria or carina ; the apical area strongly punctate, very shallowly impressed behind and there separated from the scrobe by a low narrow carina. *Antennae* testaceous, slender ; the scape exceeding the front margin of the prothorax, abruptly clavate, with sparse erect setae ; the funicle with joint 1 slightly longer than 2, the distal joints much longer than broad and clavate. *Prothorax* transverse, strongly rounded laterally, widest behind the middle, broadly but shallowly constricted at the apex, the postocular lobes feeble ; dorsum almost flat in the middle line, with fine shallow punctures which are longitudinally confluent and completely hidden by scaling, without any median carina or stria, and with sparse long erect setae. *Elytra* ovate, widest at one-fourth from the base, slightly narrower and more compressed behind in the ♂, the base jointly sinuate ; the fine shallow striae containing small separated punctures which are entirely hidden by the scaling, only the minute recumbent seta in the punctures being visible ; the intervals broad, feebly convex, each with a single row of long erect whitish setae. *Legs* honey-brown, with dense grey scales, the femora usually with a green band and a few green scales at the apex of the tibiae ; femora edentate ; the front tibiae incurved at the apex (less so in ♀) and feebly denticulate, the hind pair strongly denticulate, the corbels normal. *Underside* squamose, without setae, except on the margins of the last ventrite, which is simple in ♂ ; mesosternum without a tubercle.

Length 4·5–5·0 mm., breadth 2·0–2·5 mm.

Orange Free State : Frankfort, 1 ♂, 2 ♀♀, vi.1936 (*J. J. Jordaan*—type) ; Bothaville, 1 ♂, 1 ♀ (*Dr. H. Brauns*).

The Division of Entomology, Pretoria, reports this weevil as damaging young maize at Frankfort.

In the Transvaal there occurs a form of this species in which the prothorax is notably narrower and usually widest at the middle ; but there are intermediate forms, and although the extremes look very different, no distinctions can be found in the aedeagus of the males. It is treated therefore as a local race.

Eremnus angustirostris articollis, subsp. n.

Transvaal : Zoutpansberg, 2 ♀♀ (*Kaessner*) ; Zeerust, Marico, 1 ♀, ii.1928 (*Prof. J. C. Faure*) ; Standerton, 1 ♂, 1 ♀, ii.1925 (*Dr. A. Ingram*) ; 1 ♂, 1 ♀, without precise locality.

This insect has a much narrower rostrum than any *Eremnus* known to me, and the only other bright green species that has been described is *viridanus*, Fhs., which differs *inter alia* in having the rostrum separated from the head by a deep lateral incision, its dorsum being broad and flat with a fine median carina, and the setae are all very short and recumbent.

Subfamily LEPTOPINAE.

Promecopsis canavaliae, sp. n. (Plate XII, fig. 4).

♂♀. Derm black, with dense light brown or grey scaling and dark brown markings ; prothorax brown or greyish brown, with a very indefinite narrow paler median stripe ; elytra with an ill-defined common transverse brown band at the base which is widest at the suture and narrows to the shoulders, and a much broader and more sharply defined dark brown band about the middle which reaches the lateral margins and is deeply sinuate on its anterior edge, the broad pale apical area more or less suffused with brown in the middle ; underside with uniform grey or pale brown scaling and the middle of the apical ventrite bare.

Head with the forehead a little narrower than the interantennal space, depressed in ♂ and flat in ♀, closely squamose, with a median stria continuous with the rostral furrow. *Rostrum* as long as broad, impressed down the middle in ♂, flat in ♀, with a deep median sulcus in both sexes, the margins of the dorsal area subcostate. *Antennae* with joint 2 of the funicle shorter than 1, the remaining joints longer than broad. *Prothorax* transverse, shorter than the basal width, with the sides strongly rounded anteriorly, widest beyond the middle, subparallel-sided close to the base ; the dorsum flat longitudinally in the middle, very rugosely punctate, without any median carina, but with a very shallow short median stria near the base ; the dense round scales partly concealing the punctures, the setae stout, brown and subrecumbent. *Scutellum* trapezoidal. *Elytra* of ♂ parallel-sided from the rectangular shoulders to beyond the middle, slightly rounded and widened behind the middle in ♀ ; the broad striae with deep round punctures which appear to be separated by at least their own length when the scaling is intact ; intervals 3 and 5 more elevated than the others in the dark brown areas but not where the scaling is pale, the sub-basal elevation on 3 being the highest ; all the intervals with a row of stout spatulate setae, which are subrecumbent in ♂ and suberect in ♀, being more numerous and irregular on the elevations. *Legs* stout, with dense grey scaling, the basal half of the hind femora light brown ; front tibiae and tarsi of ♂ normal ; anterior pairs of tibiae with small inconspicuous denticles, hind pair not denticulate. *Underside* with long narrow scales in the middle and broader ones laterally ; the mesosternal process convex but not protuberant.

Length 4·5–6·0 mm., breadth 2–3 mm.

Brazil : Bahia, 5 ♂♂ 5 ♀♀, attacking leaves of *Canavalia ensiformis* and *Erythrina*, 1936 (*Dr. G. Bondar*).

Closely allied to *P. scrobicollis*, Fhs., which differs as follows : the forehead slightly convex transversely ; the rostrum not subcostate laterally ; the distal joints of the funicle not longer than broad ; the prothorax as long as the basal width, much less rounded laterally ; the elytra with the intervals all even ; all the tibiae with a row of long sharp teeth.

Subfamily Brachycerinae.

Brachycerus citriperda, sp. n. (Plate XII, fig. 3).

♂♀. Black, with dense earthy indumentum, which is more or less tinged with fulvous on the four dorsal rows of tubercles on the elytra, and a very indistinct common transverse paler patch above the declivity extending to stria 3.

Head with shallow punctures that are entirely hidden by clothing, the forehead convex, without supra-ocular ridges, separated from the rostrum by a deep sulcus, which is, however, normally concealed by a dense covering of indumentum. *Rostrum* shorter than the prothorax, stout, almost parallel-sided in the basal half, with the genae rather abruptly and strongly dilated, subporrect at the base and somewhat abruptly curved downwards at one-third ; the dorsum with coarse confluent punctures which are normally concealed, appearing almost smooth, except for a very shallow depression on each side above the antennae and an abbreviated median stria at the base, without any basal elevations ; the epistome indistinct and not elevated. *Antennae* with the club elongate, subcompressed, parallel-sided, with a short sharp point at the apex. *Prothorax* rather longer than its basal width, strongly rounded laterally, widest at the middle ; the base depressed and shallowly sinuate in the middle, the apical margin produced and arcuate dorsally, the postocular lobes feeble ; the dorsum not pulvinate, but strongly convex longitudinally, highest at the middle, set with very deep large close punctures, appearing almost sponge-like when bare but the punctures normally filled with indumentum, the anterior margin trifoveate, the dorsal intervals on the basal half only with a few flat shiny granules that become larger laterally ; the pleurae with smaller sparser punctures and much larger flat shiny granules, about 12 in number (9 to 15) and usually arranged in three or four irregular longitudinal rows ; the short sparse dark setae subrecumbent. *Scutellum* minute and normally bearing a small tuft of erect scales. *Elytra* oblong-ovate, with irregular rows of subreticulate foveae, becoming more regular laterally ; interval 3 with nine obtuse tubercles, of which the basal one is elongate and often united with the second and the fifth is the highest of all, these tubercles being entirely covered with dense erect fulvous scaling, except two near the apex which bear a large shiny bare patch ; interval 5 with six or seven similar tubercles, bearing a shiny patch on the exterior face except the second and third and sometimes the fourth ; interval 6 with an abbreviated row of five (sometimes six) smaller and slightly more conical tubercles which are all shiny on the outer face ; 7 and 9 with complete rows of large flattened shiny granules, and 8 usually with one near the base and two behind the middle but sometimes with additional ones in between ; 1, 2 and 4 without any trace of granules ; the large dorsal tubercles in the first two rows each with two (rarely three) stout dark suberect setae, those in the third row with only a single much shorter seta. *Legs* stout, with dense uniform sand-coloured scaling and scattered stout dark setae ; tibiae with the external apical angle rounded and only the two anterior pairs with a stout mucro, the dorsal edge not carinate ; tarsi squamose above and below, with only a few stout dark setae on each side beneath. *Sternum* with a strong ridge in front of the hind coxae. *Venter* with ventrite 2 as long as 3 + 4, 3 being more depressed in ♂ than in ♀.

Length 9·5–11·0 mm., breadth 5–6 mm.

NATAL : 1 ♀, without locality ; 5 ♂♂ 1 ♀, Muden, attacking citrus, iii.1937 (*W. K. R.*). Submitted by Prof. W. J. van der Linde, University of Pretoria.

Belongs to the group of *B. peregrinus* and *ephippiatus*, Fhs. 1871, but these and the allied species described by Fåhraeus all differ in having an elevation either above each eye or on each side of the base of the rostrum.

Subfamily ACALYPTINAE.

Amorphoidea pectoralis, sp. n.

Piceous black or piceous brown, with the prothorax often paler, covered with very short recumbent golden setae which do not conceal the integument.

♂. *Rostrum* comparatively long and slender, as long as the pronotum, gently curved, very gradually widening from base to apex ; dorsum not flattened, opaque and with dense fine longitudinally-confluent punctures, except at the base which is shiny and with separated punctures, with two very shallow striae above the scrobe separated by a fine low carina. *Antennae* testaceous brown, inserted beyond the middle of the rostrum. *Prothorax* transverse (2 : 3), gradually widening from the base to the middle and there armed with a stout tooth, which projects slightly outwards with its anterior edge directed slightly forwards, the anterior part of the prothorax rounded laterally and distinctly constricted at the apex, subtruncate at base and apex, the base marginate and with a deep transverse basal stria ; the dorsum gently convex longitudinally, with dense fine shallow subreticulate punctures throughout. *Elytra* broadly ovate, with well-marked closely-punctate striae, the intervals much broader than the striae, finely rugulose. *Legs* with a very small tooth on all the femora. *Sternum* with a high flattened elevation in the middle of the prosternum just in front of the coxae.

♀. *Rostrum* a little more slender, with the antennae inserted at the middle. *Prothorax* without any lateral tooth, the apical constriction much shallower. *Sternum* without any elevation.

Length 3–4 mm., breadth 1·5–2·0 mm.

JAVA : Banjoewangi, 5 ♂♂ 1 ♀, on cotton flowers, v.1936 (*Dr. C. Franssen*).

Nearly allied to *A. bicolor*, Fst. 1899, which, however, has the thorax pale reddish yellow, contrasting strongly with the blackish elytra ; the rostrum is shorter than the pronotum and more or less flattened dorsally ; the elytra are more ampliated immediately behind the basal angles ; the front femora have no trace of a tooth ; and in the ♂ the sides of the pronotum are only obtusely angulated, without any projecting tooth, and the prosternum has no elevation.

A. lata, Mot. 1858, is also a near ally, but the ♂ has the sides of the prothorax simply rounded laterally and without any prosternal elevation, and all the femora bear a large tooth.

This genus seems to be rather specially associated with cotton flowers, for *A. bicolor* (of which *Eudela armicollis*, Lea 1915, is a synonym) was observed in these flowers by Mr. E. Ballard in Papua, and there is a similar record for *A. arcuata*, Mot. 1858, in South India.

Subfamily CRYPTORRHYNCHINAE.

Conotrachelus licaniae, sp. n.

♂♀. Derm testaceous brown, with fairly dense elongate fulvous scales more or less intermixed with or replaced by greyish white scales, especially on the upper half of the declivity of the elytra and along the sides of the carinae; prothorax with sparse fulvous setiform scales in the middle of the disk, the sides and pleurae with dense greyish white (rarely fulvous) scales, which extend on to the shoulders of the elytra; underside with less dense whitish scales and a small fulvous patch on the mesepisterna.

Head rugosely punctate, with two denser patches of fulvous scales on the vertex and a few variable raised bare spots, and a transverse impression just behind the eyes. *Rostrum* rather slender, gently curved, parallel-sided, a little longer than the head and prothorax, 5-carinate, the apical third smooth and very finely punctate in ♀. *Antennae* with joint 1 of the funicle slightly longer than 2. *Prothorax* subconical, a little broader than long (7 : 8·5), widest at the base, only slightly rounded laterally at the middle, moderately bisinuate at the base; the dorsum only gently convex longitudinally, highest at about the middle, coarsely and closely punctate, the interspaces often subcrescentic, and with a distinct median carina that does not reach the base. *Elytra* subtriangular but rather broadly rounded at the apex, widest at the shoulders, which are rectangular with the angle rounded and not projecting laterally; the punctures in the striae separated by about their own length, diminishing behind; intervals 3, 5, 7, 9 carinate throughout, the carina on 3 shallowly impressed at one-fourth from the base, 8 with a low abbreviated carina behind the middle, intervals 1, 2, 4 with a row of low obsolescent granules. *Sternum* with the front coxae narrowly separated; mesosternum broadly impressed and subtuberculate on each side; metasternum between the coxae about as long as a middle coxa, shallowly impressed in the middle of the basal half. *Legs* with fairly dense fulvous and grey scales; femora with a rudimentary second tooth; front tibiae with the external apical angle somewhat dilated; hind tarsi with joint 2 slightly shorter than 3. *Abdomen* of ♂ with the pygidium distinctly visible from beneath, the apical margin of ventrite 5 shallowly bisinuate; ventrite 5 of ♀ without lateral impressions.

Length: 5·0–6·5 mm., breadth 2·8–3·5 mm.

BRAZIL: Patos, Parahyba, 1 ♂ 1 ♀, xii.1936, 2 ♂♂ 2 ♀♀, ii.1937 (*L. Pyenson*).

Mr. Pyenson reports that the larvae of this weevil do serious damage to the seeds of *Licania rigida*, which are utilised for the production of oil.

Very closely allied to the Central American *C. lateralis*, Champ. 1904, which, however has the rostrum laterally dilated in the middle and its median carina dilated anteriorly; the prothorax is nearly parallel-sided in the basal half and more narrowed in front; the elytra are slightly wider just behind the shoulders, the lower intervals are not granulate, the carinate ones bear erect or suberect white setae, and the scales in the punctures are much longer and narrower; and the venter is only sparsely clothed with fine setae without any scales.

Catagmatus clematidis, sp. n.

♂♀. Rather dull black, entirely bare.

Head shiny, with small scattered punctures, the transverse eyes closely approximated at their inner angles. *Rostrum* short, stout, much wider in the apical half, similar in the two sexes, curved dorsally but almost straight beneath, shiny and sparsely punctate dorsally on the basal half and more closely longitudinally punctate at the sides, longitudinally striolate on the apical half. *Antennae* red-brown;

joint 1 of the funicle as long as 2–4, 3–7 transverse and progressively widening distally. *Prothorax* transverse, widest at the base, rapidly narrowing anteriorly, very feebly rounded laterally, with a broad shallow constriction at the apex ; the apical margin arcuate, the postocular lobes prominent, the base bisinuate ; the dorsum convex longitudinally along the middle line and sloping steeply near the apex, set with large elongate punctures except on a broad oblique shiny impunctate patch on each side of the basal half, with a median carina which is high on the anterior half and becomes flattened and punctate towards the base ; the pleurae with a very large deep fovea near the apical margin below the postocular lobe and with sparse sulciform punctures elsewhere. *Scutellum* small, ovate, bare, impunctate. *Elytra* subcuneate, widest just behind the obliquely prominent shoulders (which are much wider than the prothorax) and thence rapidly narrowing to the apex, the subapical lateral constriction very deep ; the whole surface very uneven, with broad shallow striae containing large deep distant foreae, which are much wider than the striae and irregularly invade the intervals, the sutural margin striate ; the alternate intervals bearing strongly sinuous carinae. *Legs* with coarse longitudinally confluent punctures or carinulate ; tibiae with a sharp angulation on the dorsal edge near the base on the posterior pairs, the angle being rounded on the front pair ; claws appendiculate.

♂. With a stridulatory file on lower surface of the elytra near the apex.

Length : 4·4–5·0 mm., breadth 2·2–2·5 mm.

SUMATRA : Soengar Aoer, Padang, 3 ♂♂ 3 ♀♀, attacking *Clematis*, viii.1930 (*Fr. A. T. H. Verbeek*).

The only other known species of the genus occurs in Japan, *Catagmatus japonicus*, Roel. 1875, and very closely resembles the present species ; it has the rostrum more strongly and closely punctate on the basal half ; the impunctate areas on the prothorax are smaller, more transverse and not shallowly impressed ; the foveae on the elytra are narrower and much more regular ; and the basal angulation on the front tibiae is sharp and not rounded.

Roelofs failed to record that the claws in his genotype are appendiculate. It may be noted that in the *Catalogus Coleopterorum* (par. 151) the name of the genus erroneously appears as *Catagnatus*.

Ocladius dianthi, sp. n. (Plate XII, fig. 5).

♂♀. Derm black, variegated with patches of fulvous and whitish scales ; prothorax with only a few scattered white setiform scales ; elytra with a very indefinite broad transverse band of fulvous and whitish scales at the base from interval 1 to 7, a similar narrower one across the middle from 1 to 6, and another across the top of the declivity from stria 1 to 3 and there continued longitudinally backwards for two-thirds the length of the declivity.

Head with coarse confluent punctation and short pale recumbent setae, the rostral carinae not ascending the forehead. *Rostrum* strongly curved, parallel-sided, with three carinae and four deep punctate sulci, the apical area in ♂ set with coarse confluent punctures and short erect setae, the punctures, smaller and separated in ♀ and the setae absent. *Antennae* red-brown, inserted at the middle of the rostrum in ♂ and a little behind it in ♀ ; funicle with joints 1–5 progessively diminishing in length and all longer than broad, 6 and 7 much shorter, equal and transverse. *Prothorax* twice as broad as long, subconical, slightly rounded laterally, widest at the base, which is truncate, constricted near the apex, which is arcuate ; the dorsum with six deep punctate sulci in the middle, separated by seven high narrow carinae, of which only the middle one is straight, the others more or less undulant and sometimes irregular, the lateral sculpture consisting of very large deep reticulate foveae. *Elytra* fitting closely to the prothorax, with the sides continuous, broadly ovate, longer than broad (6 : 5), with nine somewhat irregular rows of very large foveae, those in the first two rows being oblong and the others subquadrate ; the longitudinal intervals narrower than the foveae and very irregular, 1, 3 and 5 somewhat broader and higher than the others and rugosely punctate ; the septa between the punctures in the rows mostly as high as the higher intervals and often uniting laterally to form irregular transverse ridges, those in rows 3 and 4 bearing rather shiny granules towards the apex, and those in rows 5 and 6 with large prominent tubercles behind the middle ; interval 1 markedly dilated at the base, the sutural margin having a fine carina on each side from near the base to the middle, behind which the suture is broadly depressed to the apex. *Legs* black, with a narrow band of elongate pale scales on the posterior pairs of femora, and an elongate patch of fine pale fulvous setae on the apical half of the outer face of the tibiae ; femora with punctate sulci throughout, the dorsal ones being shallower ; front tibiae with a broad sulcus and two sharp carinae dorsally, the posterior pairs not sulcate dorsally but with a strongly denticulate carina. *Sternum* with the pectoral furrow not sharply delimited behind, but continued shallowly to the hind margin of the metasternum. *Venter* with ventrite 2 separated from 1 by an obtuse carina, sloping steeply backwards and mostly impunctate.

Length 4·5 mm., breadth 2·5 mm.

UNION OF SOUTH AFRICA : Warmbaths, Cape Province, 11 ♂♂ 8 ♀♀, v.1937 (*C. C. Hattingh*).

The larvae of this species are reported by the Division of Entomology, Pretoria, as boring in the stems of carnations.

Belongs to the group of *O. subundulatus*, Fhs. 1871, and is nearly allied to *O. rupicola*, Hesse 1928 ; but in the latter species the foveae on the elytra are smaller, the intervals broader and much more regular, interval 1 being parallel-sided at the base, the scaling is denser and more extensive, the scales being nearly twice as long, the sutural impression is clothed with dense fulvous scaling from the middle nearly to the apex, the tubercles on the septa in rows 5 and 6 are only about half as large, etc.

Subfamily BARIDINAE.

Thegilis theobromae, sp. n.

♂♀. Rather shiny black, with sparse fulvous scales, which are unevenly distributed on the elytra so as to form indefinite transverse markings ; sternum with sparse grey scales, the venter simply setose.

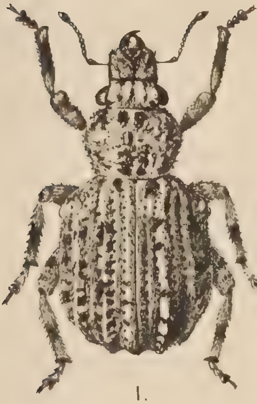
Head with very coarse subconfluent punctures, the narrow forehead almost entirely occupied by a smooth carina continuous with that on the rostrum and terminating above in a very large deep triangular fovea. *Rostrum* with three smooth carinae on the basal half and elongate punctures between, a broad lateral sulcus above the scrobe containing two rows of punctures. *Prothorax* transverse (2 : 3), widest at the base narrowing in a curve to the apex, which is briefly and shallowly constricted ; the apical margin gently arcuate dorsally, the postocular lobes very feeble ; the dorsum slightly convex longitudinally, highest behind the middle, with large shallow punctures (much wider than the intervals) which become denser laterally, and with a variable abbreviated smooth median line. *Scutellum* elongate, almost diamond-shaped, widest behind the middle, the basal arm of the diamond being longer than the others, bare, impunctate. *Elytra* ovate, not much broader than the prothorax, widest behind the oblique shoulders, laterally constricted near the apex, with broad sulci containing large separated punctures ; the intervals each with a low narrow shiny carina and irregular punctures on each side of it, interval 1 flat on the basal half but with its sutural edge becoming finely carinate posteriorly. *Legs* black or piceous with the dorsal edge of the tibiae and the last joint of the tarsi red-brown, strongly punctate and with sparse stout recumbent fulvous or grey setae; femora with a stout triangular tooth, the hind pair only having an additional small one beyond it; tibiae much compressed, the dorsal edge on the posterior pairs bearing a very high sharp laminate carina which ends in two sharp teeth near the apex, the carina on the front pair much lower, ending at some distance from the apex and followed after a short interval by a single short tooth; the tibial uncus not bent inwards but continuing the long axis of the tibia and almost spatulate.

Length 8·0–8·5 mm.; breadth 4·2–4·5 mm.

BRAZIL: Bahia, 5 ♀♀, attacking buds of cacao, 1936 (*Dr. G. Bondar*—type); Espirito Santo (*Schmidt*, coll. Fry).

The genotype, *baridioides*, Champ. 1905, is a much larger insect which differs *inter alia* in having the forehead much broader and without any median carina; there is a very large fovea on the inner edge of each eye, while the frontal fovea is quite small; and the postocular lobes are dentiform, the pronotum being much more finely punctate.

The following Brazilian species of *Cryptorrhynchus* would be much better placed in *Thegilis*, viz. *austerus*, Boh. 1837, *unicolor*, Rld. 1837, and *geminatus*, Boh. 1844, because they have the same Barid-like facies, with comparatively narrow shoulders and the high laminate carinae on the tibiae. It is true that *geminatus* has no tooth on the femora, but in *unicolor* the tooth is very greatly reduced, and the character is here of doubtful generic value.



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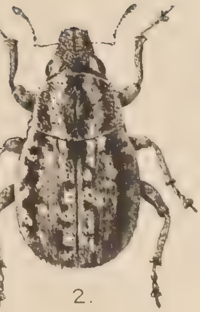

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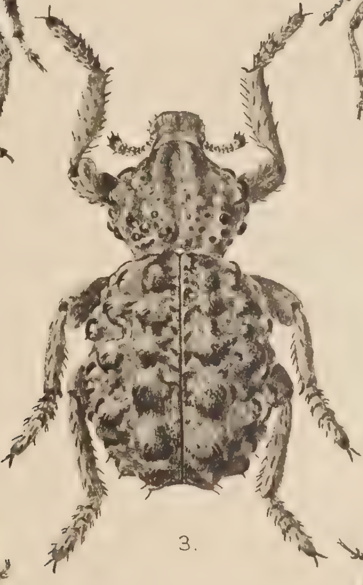

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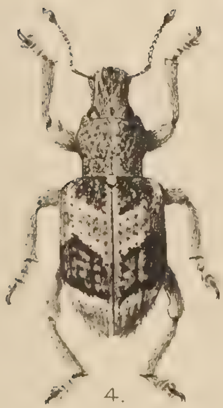

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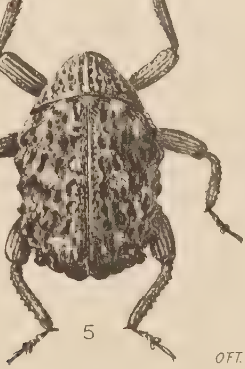

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1. *Blosyrus ipomaeae*, Mshl., sp.n.
2. *Analeucops* (g.n.) *cuthbertsoni*, Mshl., sp.n
3. *Brachycerus citriperda*, Mshl., sp.n.
4. *Promecopsis canavaliae*, Mshl., sp.n.
5. *Ocladius dianthi*, Mshl., sp.n

ROOT APHIDS AND ANTS AFFECTING RUBBER-PRODUCING PLANTS.

By M. S. Ghilarov.

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In the course of entomological investigations of the rubber-producing plants, *Scorzonera tau-saghyz*, Lipsch. & Bossé, *Taraxacum kok-saghyz*, Rodin, and *Taraxacum megalorhizon*, Hand.-Maz., at the Ukrainian Rubber-Plants Experimental Station (near Kremenchug), it was discovered that the destruction of these plants can be caused by root Aphids and the ants associated with them.

The following species of root Aphids are being found on the roots of rubber-producing plants: *Trifidaphis phaseoli*, Pass., *Trama troglodytes*, Heyd., *Aphis plantaginis*, Schrk., and *Xerophilaphis scorzonerae*, Mordv.*

Of these, *Trama troglodytes* and *Aphis plantaginis* have little significance, as their colonies are not very numerous and they are found on roots infested by other species. *Trifidaphis phaseoli*, which sucks the thin lateral roots, is of more importance. The parts of the roots situated distally from the places where the Aphids suck die off, and plants that are not fairly well developed are destroyed if the soil is not damp enough. For example, in some fields of the Experimental Station during the drought in 1934, up to 40 per cent. of *Scorzonera tau-saghyz* plants were infested by *Trifidaphis phaseoli* and about 17 per cent. were destroyed by it.

Of even more importance is *Xerophilaphis scorzonerae*, and as a result of the attacks of this aphis and the ants associated with it, about 60–80 per cent. of rubber-producing plants were destroyed in some fields in 1934.

Nevsky (1929), who described the genus *Xerophilaphis*, supposed that it is endemic in Central Asia. But the occurrence of *Xerophilaphis scorzonerae* on the roots of rubber-producing plants in the Ukraine, in Middle Russia and in the Northern Caucasus greatly extends the area of this genus north- and westwards.

This aphis could not have been imported from Central Asia with the rubber-producing plants, as it was not found on the roots of the wild plants—*Scorzonera tau-saghyz* in the region of the Karatau Mountains and *Taraxacum kok-saghyz* in the valley of Keghen (Semirechie). Besides, rubber-producing plants are grown on the plantations only from seeds; grafts were not imported from Central Asia. *Xerophilaphis scorzonerae* occurs in great quantities on the roots and rhizomes of the local wild Compositae (*Taraxacum officinale*, L., *T. serotinum*, W. K., *Sonchus arvensis*, L., *Hieracium* spp.) in the vicinity of Kremenchug, and also in places far removed from the fields of rubber-producing plants.

Virginiparous wingless females of *Xerophilaphis scorzonerae* differ from the other representatives of this genus by the following combination of characters: three pairs of marginal tubercles; one on the prothorax, one on the first and one on the seventh abdominal segment. The cornicles are nearly cylindrical and their length is almost equal to that of the obtuse-triangled cauda. The length of the cauda is almost equal to the width of its base. On both sides of the cauda there are about 6–7 hairs. The spine on the apical joint of the antennae is as long as the basal part of this joint; the third joint is as long as the fourth and fifth together, both being of the same size. General coloration of integument brownish-green, the whole body being covered with rather bright azure-blue velvet-like powder. Length of the body up to 2·3 mm. (The winged forms have not yet been described.)

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* The writer wishes to place on record his indebtedness to Dr. A. K. Mordvilko for the identification of the *Xerophilaphis* as a new species, which he has described, and for checking the identifications of other species of Aphids. The writer is also very grateful to Dr. W. A. Karavajev for the identification of the ants.

Xerophilaphis scorzonerae occurs on the roots nearly always in more or less deep cavities, which may be in the form of deep channels or holes with openings of very different sizes, the walls of the cavities being always smooth and as if polished. Sometimes the roots are so heavily infested that they look like a sponge (fig. 1).

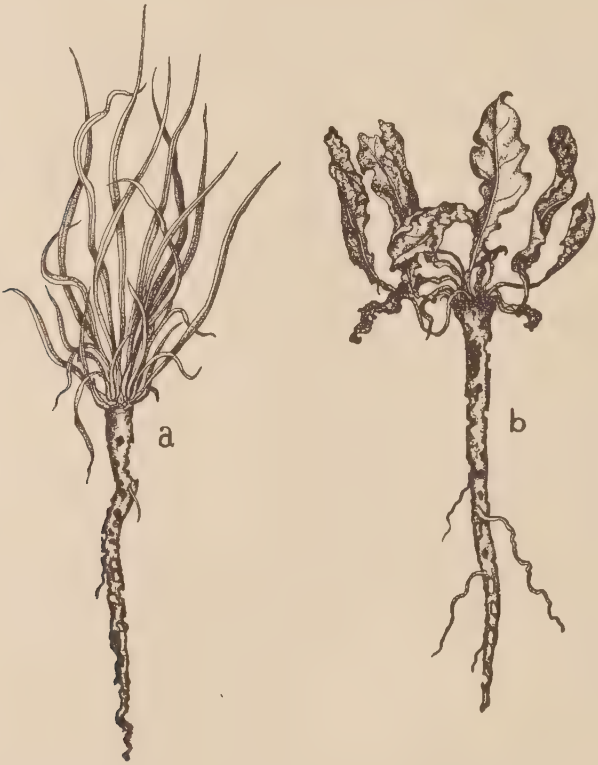

Fig. 1. (*a*) The root of *Scorzonera tau-saghyz* injured by *Xerophilaphis scorzonerae* and *Lasius niger alienus* ; (*b*) the root of *Taraxacum kok-saghyz* injured by the same insects.

There cannot be any doubt that such wounds could not be produced by sucking insects, so that it was naturally assumed that their formation was due to the ants (*Lasius niger alienus*, Foerst.) which always associated with the Aphids when the roots were perforated. In fact, direct observations showed that these ants gnaw the roots of the plants at the spots where the Aphids have been sucking and transport the Aphids to the new places which have already been cleaned by them.

It seems that the preliminary stay of the Aphids on the root makes it more attractive to the ants, because the roots of rubber-producing plants have never been seen to be attacked by these ants without the presence of Aphids, even when growing in the very midst of ants' nests ; and on the other hand, when there were no *Lasius* ants near by, the wounds were never observed on the roots of plants infested by *Xerophilaphis scorzonerae*, which in such cases occurred at or near the surface of the soil on the upper part of the root, or at the base of the leaves. Thus the formation of the wounds is caused only by the joint action of these two insects.

TABLE I.

Date of observation	Average number of nests of *Lasius* per sq. m.	Percentage of plants infested by *Xerophilaphis*	Status of the roots with Aphids	Localisation of Aphids	Percentage of plants destroyed
3.viii.	—	80	Intact	Near rootcollar	1
1.viii.	1·2	87	With wounds	In wounds at different depths	14

As shown in Table I, the presence of *Lasius niger alienus* in fields of *Taraxacum megalorhizon* infested by *Xerophilaphis scorzonerae* determines the condition of the roots and the loss of plants: Cases of the occurrence of *Xerophilaphis scorzonerae* with other ants, and of *Lasius niger alienus* with other subterranean Aphids at the roots of rubber-producing plants, prove that the character of the damage to the roots and the localisation of the Aphids are determined by the species of associated ants. The results of such observations are shown in Table II.

TABLE II.

Root-Aphis	Ant	Localisation of the Aphids on the roots	Condition of the tap-root	Occurrence of combination
Xerophilaphis scorzonerae	*Lasius niger alienus*	In wounds on the tap-root	Injured	Very often
Xerophilaphis scorzonerae	*Solenopsis fugax*	On the thin side-roots	Intact	Seldom
Xerophilaphis scorzonerae	(ants absent)	On the root collar and at the base of the leaves	Intact	Rather seldom
Trifidaphis phaseoli	*Lasius niger alienus*	In wounds on the tap-root	Injured	Often
Trifidaphis phaseoli	*Solenopsis fugax*	On the thin side-roots	Intact	Often
Triphidaphis phaseoli	(ants absent)	On the thin side-roots	Intact	Seldom
Trama troglodytes	*Lasius niger alienus*	In wounds on the tap-root	Injured	Seldom
Trama troglodytes	(ants absent)	In different spots on the roots	Intact	Seldom
(Aphids absent)	*Lasius niger alienus*	—	Intact	Rather seldom

It is evident from the table that the two species of ants cultivate their Aphids in a different manner. Thus *Solenopsis fugax*, Latr., which is entirely subterranean, is usually associated with the Aphid *Trifidaphis phaseoli* (in the conditions obtaining in the plantations). These ants when cultivating *Xerophilaphis scorzonerae* make it live on the thin lateral roots, rather deep, *i.e.*, in places where this Aphid does not occur usually, because in the absence of ants it is to be found only on the upper part of the tap-root and even on the leaves.*

The Aphids destroy the tissue of the root by sucking, and the ants (*Lasius niger alienus*) gnaw the wounds at the points of suction and transport the Aphids into these newly formed holes.

The plants infested by these pests that are not actually killed by them are almost always damaged later by root decay.

Xerophilaphis scorzonerae is not a typical subterranean Aphid. This is indicated by its greenish colour and by the fact that it occurs on the upper part of the root if the ants are absent. It also appears on the lower surface of the leaves of dandelions and on the open central leaves of *Scorzonera*, if the moisture of the soil is adequate, as shown by observations in the field after heavy rains and in greenhouses, when the soil contained up to 90–100 per cent. of its total water capacity.

The whole life-cycle of *Xerophilaphis scorzonerae* is passed on the roots and rhizomes of different Compositae, all the known host-plants of this Aphid belonging to the Liguliflorae-Corymbiferae. On subterranean parts of these plants the eggs and wingless virginiparous females hibernate, the latter in the fissures and wounds on the roots at a depth of about 7 cm.

The reproduction of overwintered Aphids on the roots of wild Compositae and rubber-plants of the 2nd year begins in the Ukraine in the first half of April. At this time *Xerophilaphis scorzonerae* occurs only on a few plants, and reproduction is rather slow at first, but becomes more intense at the end of May and beginning of June, when both wingless and winged females emerge. Then the Aphids migrate to the new fields of rubber-producing plants. From the end of June they begin to disappear from the old plants, where they were hibernating, and their numbers increase in the fields of young plants.

Winged virginiparous females are to be found till the end of July and the first days of August, when they disappear, and the infestation of fresh plants ceases. At the same time the numbers in the individual colonies decreases, probably because the roots of the plants become coarser.

In September–October, on one plant of *Scorzonera tau-saghyz* or *Taraxacum* are to be found no more than 1–2 adults and 10–15 larvae, whilst in June–July the upper parts of the roots are entirely covered with them.

At the end of October, when the total number of *Xerophilaphis scorzonerae* has decreased to such extent that it is difficult to find them, the sexuparae emerge. At this time the pairing of winged males with wingless females was observed. Egg-laying on the upper surface of the leaves of dandelions, *Sonchus*, etc. takes place at the beginning of November.

The damage caused by *Xerophilaphis scorzonerae* is most severe in June–August. During this period rubber-producing plants infested by it are nearly always destroyed if *Lasius niger alienus* is present. For example, in one field of *Taraxacum kok-saghyz* more than 80 per cent. of the plants were destroyed by these pests (see also Gilyarov, 1935).

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* The destruction of Ragi plants by root Aphids and ants in South India has been described by Krishna Ayyar (1935). But in this case the ants were only the indirect cause of the death of the plants. Ants excavating galleries in the soil round the roots infested by Aphids (*Tetraneura ulmi*) did not affect the roots directly.

ANNOTATED LIST OF INSECTS INJURIOUS TO NATIVE FOOD CROPS IN TANGANYIKA.

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The following are the major food crops cultivated by the natives of Tanganyika :—

Maize	*Zea mays*, Linn.
Sorghum	*Sorghum vulgare*, Pers.
Bulrush Millet	*Pennisetum typhoides*, S. & H.
Finger Millet	*Eleusine coracana*, Gaerth.
Rice	*Oryza sativa*, Linn.
Pigeon-pea	*Cajanus cajan*, Linn.
Bonavista bean	*Dolichos lablab*, Linn.
Green gram	*Phaseolus aureus*, Roxb.
Black gram	*P. mungo*, Linn.
Haricot bean	*P. vulgaris*, Linn.
Lima bean	*P. lunatus*, Linn.
Cowpea	*Vigna unguiculata*, Walp.
Groundnut	*Arachis hypogaea*, Linn.
Bambarra groundnut	*Voandzeia subterranea*, Thou.
Sesame	*Sesamum orientale*, Linn.
Coconut	*Cocos nucifera*, Linn.
Banana	*Musa sapientum*, Linn.
Cassava	*Manihot utilissima*, Pohl.
Sweet potato	*Ipomoea batatas*, Linn.
Cucurbits	*Cucurbita* spp.

These crops are all either indigenous or of early introduction, except in the case of special varieties and they have achieved within the limits of their present distribution an equilibrium with their insect pests. Where there is no reasonable chance of a return for his labours, the native has ceased to grow a particular crop. This equilibrium is unstable, since pests increase in numbers at intervals owing to a variety of causes. For example, the introduction of cassava into new areas to prevent famine during the locust invasions brought to light the stem-borer moth, *Opogona chlorophanes* Meyr. In some cases cassava could not be grown and sweet potato had to be substituted. Acridids such as *Eupropacris uniformis* suddenly appear in great numbers at long intervals and do considerable damage, then disappear just as suddenly. Similarly the adverse effect of climate on the crop will render it susceptible to particular pests, especially Aphids, during periods of drought. Agricultural practice is also concerned in this equilibrium, as for example where the time of planting legumes is governed by the attacks of various Galerucid beetles, particularly *Ootheca bennigseni*, Wse., which are most active during the early rains.

The control of the pests of native food crops, not only from the aspect of preventing actual food shortage but also to increase the return for the labour expended, is a difficult problem. Since any financial transaction whatever is ruled out, even when the native has money available, the purchase of even the simplest insecticides is impossible. This is an advantage, in so far as it lays emphasis on methods of more lasting effect. Depending on detailed knowledge of the life-histories of the pests concerned, the problem has to be dealt with by improvements in agricultural practice, by crop rotations, plant sanitation, weed control, etc., and by the development of resistant varieties of plants. Here one immediately makes contact with native economy and customs, as where maize and sorghum stalks are stored for cattle food and fuel and used for screening compounds, making the rapid disposal of crop residues to reduce stalk-borer infestation very difficult.

In the following list an asterisk is used to indicate the more important pests.

The three locusts, *Schistocerca gregaria*, *Locusta migratoria migratorioides* and *Nomadacris septemfasciata* are not listed.

With few exceptions the identifications have been made by the Imperial Institute of Entomology. The list is compiled solely from the records of this Department. Pests of food in storage are not included.

ORTHOPTERA.

GRYLLIDAE.

Brachytrypes membranaceus, Dry.

Gryllotalpa africana, Pal.-Beauv.

Liogryllus bimaculatus, De Geer.

Liogryllus morio, F.

These crickets attack the young shoots of most crops, but maize in particular. They become serious when germination has been poor owing to attack on the seed by millipedes and rodents.

TETTIGONIIDAE.

Enyaliopsis carolinus, Sjöst. A wingless grasshopper, popularly included with the crickets, whose habits generally it follows. Also feeds on the leaves of mature grain crops but rarely in sufficient numbers to do serious damage.

ACRIDIDAE.

Acrida sulphuripennis, St. A green grasshopper feeding on maize leaves.

**Anacridium moestum*, Serv. The tree locust, rarely occurring in swarms, but then injurious to all grains and to a large extent legumes.

**Chrotogonus rotundatus*, Kirby. Feeds on the young leaves of legumes, particularly during very dry weather.

**Eupropacris spectabilis*, Wlk., and *E. uniformis*, Ramme. Two grasshoppers liable to appear in considerable numbers in certain mountainous districts, destroying grains and legumes, and disappearing again after two seasons.

Trilophidia angustipennis, Kirby. Feeds on the leaves of young legumes, often associated with *Chrotogonus*.

**Zonocerus elegans*, Thnbg. The elegant grasshopper; attacks all food crops except sweet potato, and is especially attracted to cassava.

THYSANOPTERA.

Hoplandothrips cahirensis, Trybom. Frequently numerous in heads of *Pennisetum*, and believed to be a cause of failure to set seed.

Physothrips sjöstedti, Trybom. In flowers of dolichos bean.

Thrips kikuyuensis, Trybom. In flowers of dolichos bean.

RHYNCHOTA.

PENTATOMIDAE.

Agonoscelis versicolor, F. On sorghum and pennisetum heads, feeding on the immature seed.

Antestia cincticollis, Schaum. On eleusine heads, feeding on the immature seed.

**Brachyplatys testudo-nigra*, De Geer. On lima and dolichos beans, frequently numerous on the green pods, causing brown spotting of the pod and shrivelled beans.

Callidea dregei, Germ. On immature sorghum heads.

Caura rufiventris, Germ. On immature sorghum heads.

**Coptosoma confusa*, Mont. On dolichos bean and cowpea pods; cause brown spotting of the pod.

**Nezara chloris*, Westw. Green stink bug; feeds on the green pods of cowpea, causing the seeds to shrivel.

**Phricodus hystrix*, Germ. The sesame capsule bug; causes the capsules to dry out without setting seeds.

COREIDAE.

Anoplocnemis curvipes, Sch. Attacks cowpea, causing malformation and death of green shoots, and injury to pods. Also found on sorghum and maize without noticeable effect.

CAPSIDAE.

Lycidocoris mimeticus, R. & P. On sesame, causing spotting and malformation of the foliage.

CERCOPIDAE.

**Locris neumanni*, Jac. On rice, particularly in nurseries, causing yellowing of the foliage.

CIXIIDAE.

Oliarus sp. Feeds on the stem and roots of rice below the soil, causing serious wilting.

DELPHACIDAE.

Peregrinus maidis, Ashm. Maize leaf-hopper.

JASSIDAE.

Cicadulina mbila, Naude, and *C. zeae*, China. These Jassids are associated with streak disease.

DERBIDAE.

Diostrombus abdominalis, Dist. Causes yellowing of the foliage of young coconuts.

ALEURODIDAE.

Bemisia sp. A suspected vector of cassava mosaic, in the absence of which it is apparently quite harmless.

APHIDIDAE.

Aphis maidis, Fitch. The common green-fly of sorghum, maize and pennisetum.

**Myzus persicae*, Sulz. The sesame aphis; a serious pest causing malformation of the plant.

COCCIDAE.

Aulacaspis tegalensis, Zehnt. Sugar-cane.

Ceroplastes stellifer, (West) Ldgr. Coconut.

Chrysomphalus rossi, Mask. var. *musae*, Laing. Banana.

Ferrisia virgata, Ckll. Cassava.

Hemiberlesia lataniae, Sign. Coconut.

**Lepidosaphes* (*Coccomytilis*) *dispar*, Vayss. On cassava stems; aggravates the effects of drought, causing the stems to dry out.

**Pseudococcus brevipes*, Ckll. Common root mealy-bug, attacking pigeon-pea; may cause the death of the plant after first year. Also on groundnuts, causing discoloration of the seed pods.

Saissetia hemisphaerica, T. T. Banana.

DIPTERA.

TRYPETIDAE.

**Dacus* spp. Puncture the young fruits of cucurbits, and in many localities preventing the growing of all but the coarsest varieties.

AGROMYZIDAE.

**Melanagromyza phaseoli*, Coq. Larvae boring in the stems of haricot beans at the collar, causing total loss of crop.

ANTHOMYIIDAE.

**Atherigona indica*, Mall. Larvae destroying hearts of young sorghum when quick maturing varieties are planted late in the season to obtain second crop.

HYMENOPTERA.

TENTHREDINIDAE.

Athalia sjöstedti, Kun. Maize sawfly, more commonly found on crucifers.

LEPIDOPTERA.

LYONETIIDAE.

Decadarchis minuscula, Wals. Small nut borer of coconuts.

**Opogona chlorophanes*, Meyr. Cassava stems and tubers are tunnelled by the larvae of this moth, with subsequent rotting due to entry of fungi and bacteria.

GELECHIIDAE.

Sitotroga cerealella, Ol. The Angoumois grain moth, the larvae of which feed on sorghum heads of the dense-panicled varieties, usually when extrusion from the terminal leaf is incomplete, owing to stalk-borer damage.

PYRALIDAE.

**Antigastra catalaunalis*, Dup. The sesame webworm feeds on the terminal leaves, webbing them together and causing malformation. Frequently follows attack by sesame aphis.

**Diatraea argyrolepida*, Hmpsn. Spotted stalk-borer of maize and sorghum, takes the place of *Busseola fusca* in the eastern parts of the Territory, but is not so destructive.

Marasmia trapezalis, Guen. A minor pest of maize leaves.

NOCTUIDAE.

**Busseola fusca*, Fuller. Maize stalk-borer, also feeding on sorghum, pennisetum and sugar-cane.

**Euxoa segetum*, Schiff. A maize cutworm.

**Heliothis obsoleta*, F. Maize earworm, also attacking sorghum, pennisetum and legumes. A single caterpillar will destroy large numbers of pods of pigeon-pea and chick-pea.

**Laphygma exempta*, Wlk., and *L. exigua*, Hübn. The army worms attack all grain and leguminous crops.

Sesamia calamistis, Hmpsn. Rice borer, occasionally found in maize stems.

SPHINGIDAE.

Hippotion celerio, L. The large caterpillars of this hawk-moth feed on young maize and sorghum plants.

LYCAENIDAE.

Virachola antalus, Hopf. A caterpillar feeding in the immature pods of haricot beans, destroying the seeds.

NYMPHALIDAE.

**Acraea acerata*, Hew. Defoliates sweet potato.

COLEOPTERA.

COCCINELLIDAE.

Epilachna chrysomelina, F. Cucurbits, cowpea.
Epilachna similis, Thnbg. Maize.
Oidosoma spilota, Baly. Sesame.
Solanophila zuluensis, Crotch. Maize.
Leaf-eating beetles, the larvae having similar habits.

MELOIDAE.

Coryna apicicornis, Guér., and *C. languinosa*, Gerst. Groundnuts.
Mylabris bizonata, Gerst. Sorghum, maize.
Mylabris dicincta, Bert., and *M. oculata*, var. *tricolor*, Gerst. Legumes.
Mylabris serricornis, Gerst. Sweet potato.
Zonitomorpha attelaboides, F. Sesame.
Zonitomorpha tenuicollis, F., var. *cylindricollis*, F. Maize.
All these Meloid beetles attack the blossoms.

LAMIIDAE.

**Ceroplesis signata*, Waterh. On pigeon-pea, ringing the stems of mature plants.
Stenodontes downesii, Hope. An occasional coconut stem-borer.

LAGRIIDAE.

Lagria villosa, F. On maize, feeding on the leaves.

EUMOLPIDAE.

Pagria sp. On lima bean leaves.

CHRYSOMELIDAE.

Chrysolina clarki, Baly. Maize.
Mesoplatys ochroptera, Stål. Legumes.
Leaf-eating beetles, of importance when the crop is young.

GALERUCIDAE.

Asbecesta cyanipennis, Har. Cowpea.
Diacantha conifera, Fairm. Cowpea.
Leptaulaca africana, Ws. Cowpea.
Leptaulaca delata, Er. Legumes and bambarra groundnut.
Leptaulaca viridula, Er. Sweet potato.
**Hallirhotius africana*, Jac. Legumes.

Hyperacantha diffusa, Ws., and *H. duplicata*, Gerst. Sweet potato.

**Ootheca bennigseni*, Ws. Legumes.

These leaf-eating beetles are serious when the host-plants are small. Early plantings of legumes are frequently completely destroyed by *Ootheca*.

HALTICIDAE.

**Aphthona bimaculata*, Jac. The sesame flea-beetle ; very destructive to the leaves.

CASSIDIDAE.

Aspidomorpha punctata, F., *A. cincta*, Ws., and *A. hybrida*, Boh.

These beetles are active during the rains, feeding on the leaves of sweet potato and retarding the development of the crop.

BRUCHIDAE.

**Bruchus obscurus*, Fhs. Defoliating lima beans.

CURCULIONIDAE.

**Alcides dentipes*, Oliv. The groundnut stem-girdler ; also destroys young sweet potato plants.

**Alcides arcuatus*, Boh. The cowpea stem-girdler.

Alcides erythropterus, Chev. An occasional stem-girdler of dolichos beans.

**Apion ugandanum*, Wagn. Attacks the developing pods of the bambarra groundnut. It is restricted to Bukoba district, where it is very active.

Baris helleri, Hartm. Sesame.

**Blosyrus angulatus*, Gerst. Sweet potato leaf weevil ; causes intense defoliation at times.

Calandra oryzae, L. On sorghum heads which have not developed fully, often as a result of stem-borer injury.

Cosmopolites sordidus, Germ. The banana weevil ; bores into the corm, causing decay and death of the plant ; fortunately not widely distributed.

**Cylas compressus*, Hartm., *C. puncticollis*, Boh., and *C. formicarius*, F. The sweet potato weevils attack the tubers in the ground and continue to develop after they have been lifted for storage. *C. compressus* is the common form, the others being restricted to Bukoba.

Diocalandra frumenti, F. Coconut.

Gyponychus quinquemaculatus, Hust. Pigeon-pea.

**Phacemastix picta*, Hesse. Sesame stem-borer. The larvae bore in the stem in numbers, with the result that the plants blow over and break.

Rhina amplicollis, Gerst. Coconut stem-borer.

Rhynchophorus phoenicis, F. Coconut weevil borer.

Sphrigodes globulus, Mshl. Defoliates groundnut and sesame.

Sphrigodes crinitus, Mshl. Defoliates sesame.

**Systates alticollis*, Mshl. Defoliates groundnut.

Systates minimus, Mshl. Defoliates lima bean.

DYNASTIDAE.

Oryctes boas, F. An occasional coconut stem-borer.

**Oryctes monoceros*, Ol. The rhinoceros beetle of coconuts ; a serious pest of neglected plantations.

THE VARIETIES OF *ANOPHELES MACULIPENNIS* IN A REGION OF GREEK MACEDONIA.*

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By J. B. Rice & M. A. Barber.

The following observations on *Anopheles maculipennis* were made during the five-year period 1932–1936 in a region of Greek Macedonia which adjoins the Aegean Sea and is limited by the Nestos River on the east and by the eastern border of the valley of the Strumon on the west. Its length is approximately 40 kilometres and it extends about 20 kilometres into the interior. It contains one large river, the Nestos, several smaller streams, several swamps, two large plains, and a great variety of hills and mountains. We are particular to define the region where we made these observations, since our findings may not be valid generally, even in Greece.

The forms of *maculipennis* with which we deal are those usually described as the varieties *messeae* and *typicus*, which are distinguished almost wholly through egg characteristics. We speak of our local forms as varieties for convenience sake, without assuming that we know definitely whether they are true varieties, species, or merely variations.

Variability of the Varieties of Anopheles maculipennis.

We found in the region surveyed many intermediate forms between typical *messeae* and *typicus*. These variations are shown in Table I. Under " surface pattern " in this table are arranged various classes, A to F. In class A, eggs conform closely to the typical form of *A. maculipennis typicus*. They exhibit dorsally two black bands and somewhat blackened tips. The portion between the bands is almost white, and the area between the bands and the tips is also nearly pure white. Eggs in class F are nearly black, the bands are not well marked, and the white portions are scattered in irregular patches, sometimes sharply marked from the blacker background and sometimes not. Between these two extremes are classes B, C, D and E, intermediate types, which in the order named pass from the *typicus*-like to the *messeae*-like forms. Those grouped under the letters A, B and C are labelled the " *typicus* group," since they are more apt to be classed as *typicus* than *messeae* ; those under D, E and F are called the " *messeae* group " for an analogous reason. The term " *typicus*," as used in this paper, may refer to any member of the *typicus* group, and the term " *messeae* " to any member of its group.

Under " float character " we have six classes, all based on the number of striae (the " roughness ") of the median chambers of the floats as seen dorsally under the high dry objective ($\frac{1}{6}$ inch) of the compound microscope. Those under class No. 1 are either completely free from striae or have not more than two or three transverse lines visible from above. They characterise eggs commonly designated " smooth." Those under class No. 6 have striae so numerous and branched that they are difficult to count and give the characteristic ground-glass appearance of the " rough " egg. Classes No. 2 to 5 have intermediate degrees of roughness, progressively greater as one proceeds to the left.

It is impossible in small space to describe accurately either the classes under the surface pattern or those under the float character. All determinations were made by one of us. For the colour pattern we made much use of figures in order to standardise our classes. The float classes were more difficult to standardise. By counting the striae in certain specimens we established our norms, and we tried to keep them constant by frequent comparisons of our findings. Both types of class were sufficiently well defined to serve for the purpose at hand—to get some measure of the variation of eggs.

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* The studies and observations on which this paper is based were conducted with the support and under the auspices of the International Health Division of The Rockefeller Foundation, and with the co-operation of the School of Hygiene at Athens.

The numbers within the table represent ovipositions or layings of eggs, each often consisting of 200 or more eggs. The characteristics of all the eggs of each batch were usually nearly uniform, so that only samples of each laying were examined. In all, this table represents many hundreds of examinations. Nearly all of the layings were obtained in the laboratory from *Anopheles* collected in village buildings, usually houses or stables.

It is seen in this table that there are many intermediate forms of both pattern and floats between our *typicus* and *messeae*. Either float or pattern classes arrange themselves into two-peaked frequency polygons. If one is to make a variety *messeae* or *typicus* from these findings only, one must use statistical means. There is evidently a correlation of *typicus* and rough floats, and of *messeae* and smooth floats.

TABLE I.

Table relating the Float Characters and Surface Marking of the Eggs of A. maculipennis.

Surface pattern		Float character						Total
		6	5	4	3	2	1	
typicus group.	A	3	11	82	32	11	—	139
	B	5	20	109	34	8	—	176
	C	3	11	37	21	6	2	80
messeae group.	D			2	15	22	17	56
	E			5	40	125	96	266
	F					19	13	32
Total ...		11	42	235	142	191	128	749

Unfertilised Generation.

Our next step was to determine if the characteristics of any of these variations persisted into the next generation. We did not succeed in obtaining crosses between *typicus* and *messeae*, so we depended on the eggs of unfertilised females. In the first generation these should not differ from the fertilised ones, since eggs are normally not fertilised until the time of laying. Ovipositions were obtained in the laboratory, the egg-type recorded, and the specimens reared to maturity. The unfertilised females were given from one blood meal to several such meals, and eggs were obtained. We succeeded fairly well in obtaining these unfertilised eggs ; in one case as many as 12 daughters of the same parent laid such eggs.

In all, we obtained and studied 38 daughters of 7 *typicus* parents, and 46 daughters of 22 *messeae* parents. All the daughters of *typicus* parentage laid eggs like those of the parents, but in three cases daughters of *messeae* parentage laid *typicus* eggs. The details of these cases follow :—

1. From a typical *messeae* parent, the eggs with smooth floats, were reared five daughters which laid unfertilised eggs. Of these five, three laid eggs of the *messeae* pattern with smooth floats like those of the parent ; while the other two laid eggs of a plainly *typicus* pattern but with smooth floats. Eggs of these two were uniform throughout the batches.

2, From a parent with a pattern intermediate between *typicus* and *messeae* but such as would be classified " D " of Table I, *i.e.*, of the *messeae* group, were reared several daughters, of which one laid a batch of eggs all of plainly *typicus* pattern with rough floats.

3. Fourteen batches of *messeae* eggs, all examined microscopically, were placed in a tank in the open. The tank was covered by a screen which was kept locked. Among the daughters reared in this tank, 11 laid unfertilised eggs like those of the parent, but a twelfth laid a batch with rough floats. All of these eggs with rough floats had *messeae* patterns except one, in which the pattern was plainly *typicus*.

While the number of these type-changes is not large, they form a fairly high percentage of all the unfertilised layings. We could not always keep these experiments under control as exact as that of bacteriological cultures, but it is unlikely that the " transformations " were due to error. At all events, it will be noted that the change was always in the direction, *messeae* to *typicus* ; there were none in the other direction. In certain egg-type changes of the total population found in natural habitats, to be described later in this paper, we note that the change was in the same direction, a suggestion that we may have to do in both instances with a reversion to an earlier *typicus* type.

Breeding-places of the Larvae of typicus and messeae.

The nature of the egg-types in the various localities were determined in two ways—by ovipositions of adults collected in neighbouring villages, and from eggs collected on the surface of the water at the breeding-places. The proportion of *typicus* and *messeae* eggs as determined by these methods was not the same in all localities. As an illustration of the variation in this proportion, we take the surveys made through a period of years along the Nestos River in our region. At Paradeisos, where the river emerges from the mountains, a locality rich in springs, we find a great preponderance of *typicus* eggs, although *messeae* is sometimes found there. Some 5 kilometres farther down the river is a hilly area in which occur many lakes and ponds. These bodies of water resemble lime sinks (limestone is abundant in the locality) in which the water is impounded and not renewed continuously by springs. There, year after year, the egg-type was consistently *messeae* ; only recently have eggs of the *typicus* type more frequently appeared. Near this locality a ditch takes turbid water from the Nestos River and conducts it across the alluvial plain below. About 5 kilometres below the source of this ditch is the village of Kineze, where water has been allowed to escape from the ditch and form a shallow, weedy pond. There the egg-type has been mixed, *typicus* and *messeae*, *typicus* greatly predominating through several years. At about the same latitude the river itself forms a series of shallow ponds or lagoons, all renewed at the time of the spring freshet but often stagnant or semi-stagnant during the summer. In these, the egg-type is also mixed, *messeae* and *typicus*, but the proportion of *messeae* is larger than is the case at Kineze. Five or six kilometres farther down, near the mouth of the river, are many shallow lagoons and pools similar to those above, except that they are nearer the sea and farther from the mountain sources of the stream. Salt water sometimes invades this area, but many ponds and pools contain fresh water. In some of these fresh ponds *messeae* has greatly predominated year after year.

It is seen that water of springs and streams, and even that of a muddy river, is favourable to the *typicus* egg-type, whether it be found in hills or plains ; while water more permanently stagnant is favourable to *messeae*, although such water may occur among hills. Generally, however, *messeae* water occurs more often in the plains, and *typicus* water among hills. In our surveys of villages in the hilly regions we occasionally find collections which yield only *typicus* eggs. But with one possible exception, we have never, despite careful search year after year, found a locality in which *messeae* eggs might not be observed either in ovipositions in the laboratory or among collections made in the breeding-place. The exception noted is that of small pools in the clear mountain streams commonly productive of *superpictus*. There we have found only *typicus* eggs ; but in these pools *maculipennis* eggs are usually few and our collections less extensive.

On the other hand, even in localities where *messeae* dominates, there is always, in our region, a large percentage of *typicus*. Where ovipositions are obtained from adult *maculipennis* collected in villages, this proportion usually exceeds 20 per cent.

Changes in the Egg-type of a Locality.

We have encountered several localities in which the egg-type has changed during the past five years. In one such locality (Mavrolefki) *messeae* dominated in 1932 ; in 1934 we found only *typicus* there. The nature of the breeding-places in the vicinity had changed in a way favourable to *typicus* ; swamps had dried up, but a stream had persisted.

In a second locality, the lake and pond region mentioned in connection with the survey along the Nestos River, there has been a tendency to increase in the *typicus* egg-type. This change has coincided with the occurrence of increased rains, which have raised the level of these lakes and ponds.

In a third locality (Datos) the change in the character of the breeding-place has not been so clearly marked. The bodies of stagnant water persisted, but their level was at times lowered by drought and at other times raised by rains or by temporary engineering operations. The proportion of fresher water has, on the

TABLE II.

Number of Ovipositions and Type of Eggs of A. maculipennis *in the Village of Datos. Change in type within the Period* 1932–1936.

Year	*typicus*	*messeae*	Percentage *messeae*
1932	1	71	98·6
1933	4	129	97·0
1934	2	5	71·4
1935	72	38	34·5
1936	47	13	21·7
Totals ...	126	256	66·9

average, increased during the five-year period. The change in the egg-type of this locality is shown in Table II, where only ovipositions in the laboratory are shown.

The only factor common to all *messeae* breeding-places in the region studied is the presence of water more or less permanently stagnant. With a dilution of this water by rains or from other causes, the proportion of *typicus* tends to increase. This condition of things is not wholly universal. It is difficult to see why a type of stagnant pool in one part of the bed of the Nestos River should have mixed egg-types year after year, while in the same kind of pool near the sea *messeae* should occur in nearly pure culture.

Neither variety seems to be adapted to brackish water, though *messeae* may occasionally breed in it. We once bred out a lot of pupae collected in brackish water. Of the *maculipennis* females thus obtained, one was made to lay unfertilised eggs, which proved to be *messeae*. In the spring, brackish ponds often have many eggs of *typicus* mixed with those of *elutus*, but we have never proved that such eggs go through all of their development in brackish water.

We find both types of egg common in sun and in shade ; possibly in full shade *messeae* occurs more often than *typicus*. There is no species of aquatic vegetation which seems more favourable to one type than to the other ; at all events, none effective through a period of years. Both types are commonly associated with *elutus*. Though *typicus* often occurs in streams with *superpictus*, *messeae* does so rarely, if ever.

One might assume that the distribution of eggs in various habitats is due to the selection of places of oviposition by females of the respective varieties. We must keep in mind, however, that we deal largely with a single variable characteristic, and we must enquire into the possibility that the environment determines the egg.

In one experiment (the tank experiment mentioned in connection with the experiments on unfertilised parents) we have reared *messeae* in a *typicus* environment. The *messeae* eggs were obtained from females collected in an environment where *messeae* predominates and were selected microscopically for the experiment. A large tank, fed by water from an underground spring, was thoroughly cleaned and sterilised of eggs by gasoline. It was covered by a screen to prevent the access of mosquitoes from the outside. The *messeae* eggs were placed in the tank, their larval development was watched, and the pupae were collected and bred out. As stated above, 11 of 12 ovipositions obtained from these bred-out *messeae* were true to type, only one showing a tendency to take on *typicus* characteristics. There was, then, in one generation little change of *messeae* in the new environment.

Attempt at Cross-breeding under Natural Conditions.

Our attempts at obtaining cross-breeding of *typicus* and *messeae* in captivity had failed, so we tried to bring about the fertilisation of *typicus* females by *messeae* males through the introduction *en masse* of the latter into a *typicus* locality. Lefki Alpha, a village situated on a flowing stream, was selected for this experiment. We have but rarely found any variety there except *typicus*. During July 1936, we obtained 335 ovipositions from females collected in this village. Every one proved to be *typicus*. During the succeeding six days we collected approximately 1,000 males from villages far distant in which over 90 per cent. of the *maculipennis* was *messeae*. We released these after sundown in Lefki Alpha, about one-half in the village itself and one-half at the breeding-place closely adjoining.

During the next 18 days we obtained 243 ovipositions from *maculipennis* females collected in Lefki Alpha and compared them with those obtained before the introduction of the foreign males. Only two ovipositions proved to be *messeae*, all the rest were *typicus* as regards both surface pattern and floats. There was not even an increase in transitional forms suggestive of hybridization. Ten days before the introduction of the males of *messeae*, a heavy rain had flushed out the breeding-place, so that the newcomers had fewer competitors among the local *typicus* males. Ovipositions obtained in Lefki Alpha later in the season gave no indication of hybrids which might appear in the second or a later generation.

The results of this experiment are essentially negative. The method, however, we believe to be a good one, since the sexes are brought into contact under more nearly natural conditions. It is quite possible that among insects brought into artificial propinquity crosses may be obtained which rarely or never occur in nature, a phenomenon not unknown among higher animals. A transfer *en masse* of *typicus* males into a *messeae* region would be worth trying.

The Effect of Temperature and Season on Egg-types.

We know from the experiments of Mer and others that both colour and floats of *A. elutus* may be modified by temperature. We confirmed this finding by obtaining successive layings of identical females kept under different temperatures. The lower temperatures favoured a darker colour with a fuller development of floats. We made similar experiments with female *maculipennis* collected in the open in spring. A protocol is given of one experiment: a female *typicus* containing mature eggs was taken on 22nd March and laid a batch of eggs on 27th March. The general colour of these eggs was very dark. After a blood meal the mosquito was kept in a room slightly warmer than the temperature in the open. There it laid a batch of eggs almost identical with the first. It was then given a second blood meal and placed in an incubator kept at 19° to 23°C. It laid a third batch of eggs on 11th April. These resembled the first and second batches except that they were considerably lighter in colour, that is, the columellae were longer. The floats and basic pattern of the eggs were the same in all three batches.

We tested second or third layings of about 19 female Anophelines, *elutus* or *maculipennis*. We confirmed the finding of Martini that overwintering females of both species may lay two or more batches of eggs, so that we could do these experiments in early spring on overwintering females as well as on those collected later in the season. In no experiment could we detect in the eggs of *maculipennis* any such radical change due to changes in temperature as are found in *elutus*. Higher temperatures favoured a lighter colour in eggs of both species but did not alter the pattern or roughness of the floats of *maculipennis*. The transformation of the colour pattern in *maculipennis* was sometimes striking. A dull dark egg of uncertain classification could be transformed into a bright one plainly *typicus*. It became very evident that general colour cannot be relied upon to distinguish varieties unless seasonal changes are likewise taken into account.

With regard to seasonal variation under natural conditions, we have the records from 6 villages in which ovipositions were obtained throughout the year and in sufficient numbers for comparison. The findings are shown in Table III. Villages are arranged in the table in the order of prevalence of *messeae* in them.

Much variation appeared among the several villages in the seasonal occurrence of the varieties of *maculipennis*, but in all cases the percentage of *messeae* in spring and summer tended to be higher than that in autumn and winter. In several cases in late autumn and winter we have found only *typicus* in bodies of water which, during the summer, had contained a mixture of both varieties.

Both varieties of *maculipennis* may be made to lay eggs in winter by keeping the adult females in an incubator for a few days and providing them with fresh blood meals. *A. m. typicus*, however, will lay eggs in the open during every month of the winter. We have found them in January and February in small numbers and only in one locality, a ditch containing seepage water and well provided with algae. This ditch is situated in the immediate neighbourhood of the village of Kineze, where many adults of *typicus* pass the winter.

TABLE III.

Seasonal Variation in the Occurrence of Egg-types in A. maculipennis.

Villages from which ovipositions were obtained		Winter* Dec., Jan., Feb., Mar.	Spring April, May, June	Summer July, Aug., Sept.	Autumn Oct., Nov.	All seasons
Kineze ...	Nbr. ovipositions	296	233	401	149	1,079
	Pct. *messeae*	9·1	9·4	23·0	10·7	14·6
Kalamon ...	Nbr. ovipositions	9	73	61	1	144
	Pct. *messeae*	22·2	45·2	14·7	0·0	30·5
Datos ...	Nbr. ovipositions	10	66	38	4	118
	Pct. *messeae*	20·0	43·9	36·9	0·0	38·1
Kalyvia ...	Nbr. ovipositions	20	166	75	0	261
	Pct. *messeae*	40·0	25·9	72·0	—	40·2
Peristerion ...	Nbr. ovipositions	8	116	250	21	395
	Pct. *messeae*	12·5	19·0	56·0	33·3	43·0
Monastiraki	Nbr. ovipositions	0	103	28	1	132
	Pct. *messeae*	—	68·0	92·9	100·0	73·4
All villages ...	Nbr. ovipositions	383	1,317	1,258	220	3,178
	Pct. *messeae*	12·3	22·8	36·4	11·8	26·1

* The bulk of the mosquitoes collected in February and March consist of overwintering females. These months are therefore classed as winter months in this comparison.

Habits of the Varieties of maculipennis as regards the Transmission of Malaria.

We have found sporozoites in both *typicus* and *messeae* collected in the open. The variety was determined by oviposition and the female subsequently dissected. Infected *maculipennis* occurs so infrequently in the region studied that we could make no adequate comparison of the percentages of the two varieties infected in nature. We have found infected *maculipennis* in villages in which *typicus* was the more common variety and also in those in which *messeae* predominated, but could find no significant difference in the percentage infected. We made many determinations of the blood meals of *maculipennis* positive for man in villages where there were *typicus* and *messeae*, but found no significant difference in this respect. We could not obtain evidence from precipitin tests and from oviposition in identical individuals, for oviposition is infrequent until after blood meals are digested.

With regard to choice of daytime resting places, whether in houses or in stables, we have more definite information. We limit the following comparisons to collections in which both *messeae* and *typicus* were present in the village on the day of survey and in which ovipositions were obtained both from mosquitoes resting in houses and from those found in stables. Of our surveys, made in different localities and seasons, 42 fulfil these conditions. Of 459 ovipositions obtained from collections in houses, 173 (37·7 per cent.) were *messeae* ; of 1,071 ovipositions from collections made in stables, 396 (36·9 per cent.) were also *messeae*. There is, then, no significant difference between the varieties in this respect.

Discussion and Summary.

In summing up the results of our study of the local varieties of *maculipennis* in a region of Macedonia, we have tried to deal with the region as a thing by itself, without allowing ourselves to be influenced by what we might know regarding the varieties of *maculipennis* found elsewhere.

We found a *maculipennis* nearly uniform throughout the whole region as regards habits and morphology, and not varying greatly except with respect to one character, the sculpturing of the eggs. On the basis of this character, we may make two groups, provisionally called *typicus* and *messeae*, but we must use statistical methods to establish these two groups, for we find much variability in them. The amount of variability is not uniform over the whole region ; in some localities the egg-type is nearly all *typicus*, in others *messeae* greatly predominates. Our problem has been to test the validity of this characteristic, especially with regard to its persistence from parent to offspring and its constancy in varying environments.

We have found in the laboratory that, as a rule, an egg variation is constant through one generation ; in exceptional cases *messeae* vary in the direction of *typicus*. We have bred *messeae en masse* in a *typicus* habitat. Only one out of twelve showed any indication of change during the first generation. We have observed certain natural habitats where, in the course of a period of years, *typicus* has replaced *messeae*. There has usually been some change in the nature of these habitats. We have determined that one characteristic of the egg of *maculipennis*, the length of the columellae, may be altered by a change in temperature during the maturation of the eggs in the adult. In the allied species, *elutus*, a more radical change may be thus brought about. We have introduced the males of *messeae en masse* into a colony of *typicus* with little evidence of any influence of these males on subsequent generations.

It is possible that only by long-time experiments or observations in nature or by cross-breeding in the laboratory we may finally arrive at the solution of the local problem. Provisionally we recognise a *typicus* and a *messeae* group. There is good evidence that we deal with two things and not with a single highly variable variety ; but we doubt that our local forms have the definiteness and stability ascribed to the varieties *typicus* and *messeae* found in other countries, where environment may be more stable or where geographical isolation may have established these varieties or species more firmly. At all events, we would hesitate to admit the presence in our region of a third or fourth variety until the nature of our one or two varieties is established. It may well be that before all forms of plants and animals are satisfactorily classified we may have to define more accurately our " strains, varieties, species " and the like, and possibly devise one or more new categories to fit the variegated pattern of living things.

APPENDIX.

Technique for obtaining ovipositions in the laboratory.—A tube vial of clear glass, 2 cm. in diameter by 5 cm. in height, is provided with a small wad of dry absorbent cotton, which is pushed down into the bottom of the vial, where it occupies a space about ½ cm. deep. The mouth of the vial is then plugged with cotton. A batch of mosquitoes is lightly chloroformed and examined to determine the species or the presence of mature eggs or to obtain any other information desired. Those from which eggs are to be obtained are placed singly in the plugged vials, the cotton stopper is replaced, and the mosquitoes are left until they fully revive. Then, by means of a pipette or siphon, enough water is admitted alongside the upper plug to saturate the wad in the bottom and leave a shallow layer of water above it. About 10 per cent. more ovipositions will be obtained thus than if only just enough water is admitted to saturate the cotton. Tap water seems to be as good for oviposition as water from a breeding-place, with or without algae. The vials are then set aside at any temperature desired until laying begins. Oviposition by gravid females is sometimes begun at once. A whiff of ether will sometimes encourage oviposition and is useful when immediate oviposition is desired.

When eggs have been laid, the female, if living, may be killed with chloroform or forceps, or otherwise disposed of. The dry cotton plug is removed, and the saturated wad at the bottom is then carefully lifted with the eggs on it and placed on a slide for examination. Several wads may be placed in a petri dish and examined together ; but if the eggs are to be bred out subsequently, one must avoid the possibility of mixing eggs of different females in the bottom of the petri dish. A provisional examination of eggs may be made with the hand lens or with a low magnification of any sort without removing the dry plug. Eggs may be allowed to hatch in the undisturbed vials.

If it is desired to examine the floats or other characteristic under higher magnification, samples of eggs may be removed and placed on a slide in a drop of diluted glycerine. The eggs will readily turn dorsal side up in this liquid on account of its higher specific gravity. Small slips of filter paper are useful for transferring samples. These slips may be used once and then thrown away.

Eggs in these small vials are easily stored and transported. A permanent mount, more or less satisfactory, may be made of an oviposition by draining off the water, adding a little formalin, and stopping the vial with a paraffined cork.

Eggs can be obtained from overwintering females by incubating the mosquitoes at 19 to 23°C. for 5 or 6 days to rid them of accumulated fat and then giving them a blood meal and placing them in the vials. Unfertilised females obtained at any time of the year may not develop eggs until after they have had several blood meals.

THE EFFECT OF TEMPERATURE ON THE REACTION OF *GLOSSINA MORSITANS* WESTW. TO LIGHT.

A PRELIMINARY NOTE.

By Rupert W. Jack, *Chief Entomologist*,
and
W. L. Williams, B.Sc. (Agr.), D.I.C., *Entomologist*,
Department of Agriculture, S. Rhodesia.

In the course of studies of the behaviour of the tsetse-fly, *Glossina morsitans*, certain facts of considerable interest concerning its phototropic reactions have been established.

The reaction to light of active flies of this species at normal indoor temperatures is positive (see also Mellanby, 1936 (p. 627) in regard to *G. palpalis*). It has been found by experiments in the laboratory that if the temperature is raised sufficiently high the reaction of the flies is reversed and becomes strongly negative.

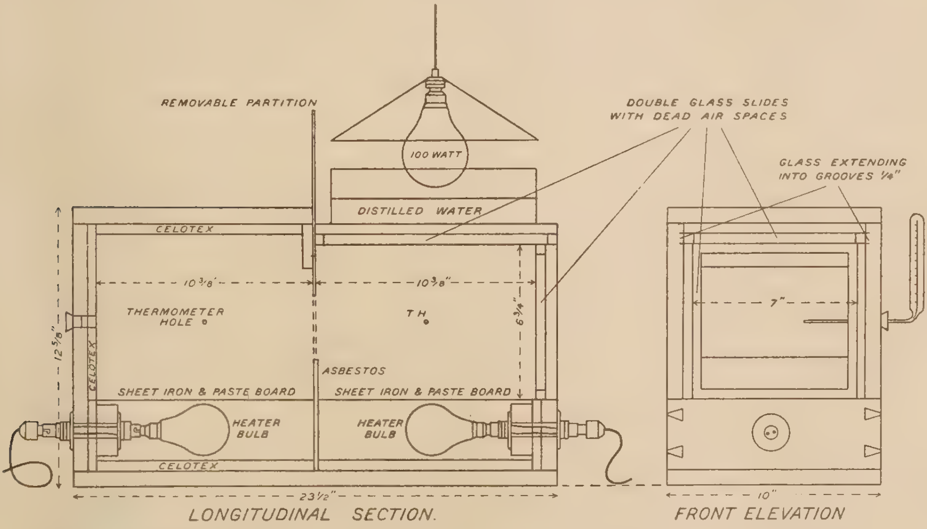
REMOVABLE PARTITION
100 WATT
DOUBLE GLASS SLIDES WITH DEAD AIR SPACES
GLASS EXTENDING INTO GROOVES ¼"
DISTILLED WATER
CELOTEX
10⅜"
10⅜"
THERMOMETER HOLE
T H
6¾"
12⅝"
CELOTEX
ASBESTOS
SHEET IRON & PASTE BOARD
SHEET IRON & PASTE BOARD
HEATER BULB
HEATER BULB
CELOTEX
23½"
7"
10"
LONGITUDINAL SECTION.
FRONT ELEVATION

Fig. 1. Apparatus used for testing the effect of temperature on the phototropic reactions of *Glossina morsitans*.

The apparatus used is shown in fig. 1. It consists of an insulated cage divided by a removable partition into two approximately equal sections. The top and end of one section are glazed, whilst all the sides and the top of the other are of wood. The floor of each cage consists of a piece of sheet iron covered with paste-board or, later, asbestos. The wooden walls are also lined with paste-board. In the light section the paste-board is white, whilst in the dark section it is blackened. Two heater bulbs are provided, one for each section, in a compartment beneath the floor. By switching on only one heater bulb the temperature of one section can be raised if necessary to a higher point than in the other. Four holes, ¾ in. in diameter, one on either side of each section of the heater compartment, are provided for observation as to the functioning of the heater bulbs or otherwise. These are not shown in the figure. The source of light mostly used in the tests has been a 100-watt electric bulb above the glass with a water screen interposed to intercept the heat rays.

The flies show no negative reaction to this light at temperatures below 30°C., but by raising the temperature to the requisite height in the light section every fly, apart from an occasional weakling which may die prematurely, can be driven into the dark section, where it will remain. A fly which has once exhibited the negative reaction will usually return promptly to the dark section if driven out, providing that the temperature remains the same or rises.

The point of greatest interest is that the reaction described takes place whether the temperature in the dark section is below, equal to, or above that of the light section.

The dominance of the impulse was demonstrated rather dramatically on several occasions, when it was found that the flies would leave an uncomfortably high but not immediately fatal temperature in the light section (*e.g.*, 42°C.) for a rapidly fatal temperature in the dark section (*e.g.*, 49°C.), dropping dead very shortly after entering the latter.

The reaction is therefore definitely negative to light itself and is independent of the relative temperature in the light and dark. The use of the water screen shows also that the light rays need not be accompanied by intensive heat rays to produce the negative reaction. In point of fact, at very high temperatures the flies exhibit a negative reaction even to the diffused daylight of the laboratory.

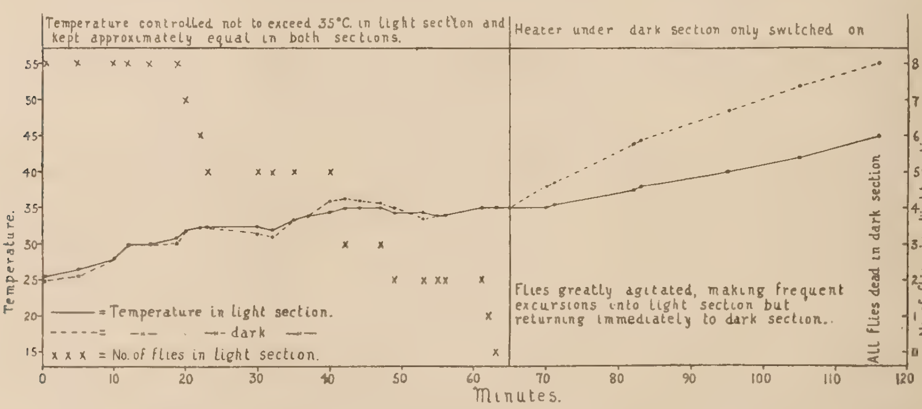

Fig. 2. Showing the slow but complete negative reaction to light of eight adult *G. morsitans* (4 males and 4 females) exposed to a temperature not exceeding 35°C., the temperature in the dark section being approximately equal to that in the light section; also the persistence of the reaction when the temperature in the dark section was raised much higher than in the light section, all the flies finally dying in the dark section.

Flies 3 days old, fed the day before the experiment.

The experiments, of which the results are graphed in figs. 2 and 3, have been selected as illustrating most of the points made. In the case of fig. 2 the temperature in the light section was kept within comparatively low limits and the reaction of the flies was slow. After all had migrated to the dark section the latter was heated rapidly to ascertain if the flies would be driven out to the lower temperature of the light section. Actually, some of the flies in their agitation dashed into the light section, but immediately returned to the dark section, usually without settling even for a moment. In the end, all died in the dark section.

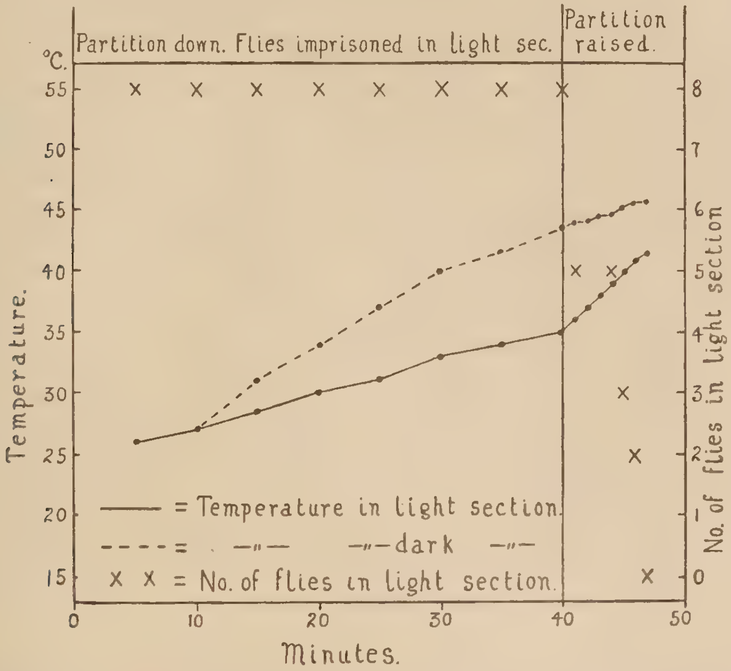

Fig. 3. Showing the rapid and complete negative reaction to light of eight *G. morsitans* adults exposed to a temperature rising rapidly from 35°C. to 43°C. The reaction takes place in spite of the fact that the temperature in the dark section is still higher than in the light section.

Flies 4 days old, fed on first and second day after emergence.

In the case of fig. 3, all the flies were imprisoned in the light section whilst the temperature in the dark section was raised. This, of course, also gradually raised the temperature in the light section, and when the latter reached 35°C. the partition was raised. All the flies migrated to the dark section within 7 minutes, although the temperature there was considerably higher than in the light section.

The 100-watt electric bulb supplied the light in both experiments. The relatively small number of flies in each experiment is due to the necessity for rapid counting.

It is of interest that the negative reaction to light is also exhibited at high temperatures by *Stomoxys calcitrans*, although not so strongly as by the tsetse.

On the other hand the common Rhodesian house-fly, *Musca vicina*, Macq., displays a far greater ability to find a more comfortable temperature by the process of trial and error independently of the light conditions, although even in the case of this species strong light may assist the search.

The difference in reaction between *Glossina* and *Musca* is, however, definite. If the temperature of both sections of the cage be raised evenly above the lethal point, the great majority of tsetses die in the dark section, whilst the great majority of the house-flies die in the light section. With *Stomoxys* a more or less even distribution has been obtained in these circumstances. On the other hand, there is some evidence that a strong light serves to guide *Musca* from an uncomfortably high temperature in the light to a considerably lower temperature in the dark. It will not, however, drive this species to an equal or higher temperature in the dark.

Both *Musca* and *Stomoxys* are much more exploratory in their habits than *Glossina*, especially *Musca*, which crawls all over the cage in and out of the two sections. *Glossina* moves mostly on the wing and is much less active, at least in confinement.

Under natural conditions, of course, the temperature in the shade is always lower than in the sun, and the reaction described above in the case of *morsitans* is obviously the guiding impulse by which the tsetse-fly is rapidly translated, when necessary, from the dangerous heat of the sun's rays to the cooler refuge of the shade.

It should be stated that experiments on the behaviour of *morsitans* under cage conditions are difficult, especially where fine distinctions in behaviour between different groups of flies are concerned. The flies tend to become sluggish and fail to respond consistently to any but very strong stimuli. They have a remarkable capacity for prolonged immobility. The flies' common reluctance to behave naturally in confinement and also the apparatus employed, preclude the possibility of exact quantitative data.

The temperature at which the negative reaction develops appears to depend somewhat upon the flies' physiological condition, especially their water content, but experiments in this connection are still proceeding. The reaction is definitely influenced by the intensity of the light and also by the length of exposure. The combination of direct sunlight and a rapidly rising temperature induces a very quick response. In the case of the average fly exposed to the light of the 100-watt electric bulb in a rising temperature migration to the dark section of the cage usually commences about 32°C. The reaction is accelerated as the temperature rises towards 40°C., when the flies tend to become agitated and obviously distressed.

In the forest the temperature in the shade is generally below that needed to induce a negative reaction to light, whilst at the same time the sun's rays are commonly sufficiently powerful quickly to raise the body temperature of the fly above the critical point, if the fly settles. In these circumstances an active fly is likely to alternate frequently in its movements out of and into shade.

Incidentally the temperature in the interior of dense patches of evergreen forest, *e.g.*, along river banks, is unlikely to be sufficiently high to maintain the negative reaction, and such patches are therefore rarely penetrated by the fly to any considerable distance.

On the other hand, during the heat of the day in the late dry season the temperature in the shade of the savannah forest not infrequently approaches and at low altitudes may even exceed 100°F. Under these conditions the flies will not stir from the shade whatever attraction in the way of moving man or vehicle may be presented. It is quite possible to drive or walk through heavily infested *morsitans* country from noon to 3 p.m. in October, for instance, and hardly to see a tsetse-fly. The immobility of the flies on these occasions is judged to be directly due to the temperature in the shade and only indirectly to the heat of the sun's rays. Consequently the alternating movement between sun and shade does not occur.

It would seem, therefore, that the distribution of tsetse-flies in relation to the vegetation and other features of their habitat at any given time may be explicable to a large extent on the basis of their phototropic reactions. Whilst the broad zones of distribution of these insects are, of course, determined by climatic, edaphic, vegetational and related factors; what may be termed their eco-distribution is, on the other hand, determined by their behaviour. We have shown that the reaction to light is much stronger than direct temperature selection. Whilst tests with a choice of humidity, except in so far as the temperature affects the saturation deficiency, have not been made, it is improbable that direct humidity selection will be stronger than the phototropic reaction. We seem here to have a dominant reaction which must inevitably exercise a very potent influence on the flies' movements and consequent eco-distribution.

Considerable interest attaches to the bearing of this reaction on the explanation of the attraction exercised on tsetse-flies by stationary traps of the Harris and other types, which either present actual shade or dark-coloured screens, etc., which look like shade. In the case of an insect such as the tsetse, a negative reaction to light will necessarily be exhibited in the field as a positive reaction towards conspicuous shade-yielding objects (Jack, 1933).

It is hoped in due course to deal with the last question and to give a fuller account of the experiments on the phototropic reactions of *morsitans* in a comprehensive report on the research work at present in progress.

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SOME INSECTS AND THEIR FOOD-PLANTS IN SIERRA LEONE.

By E. Hargreaves, A.R.C.S., D.I.C.

It is considered desirable to place on record some data relating to insects attacking economic plants in Sierra Leone ; little information has hitherto been available, and it is hoped that this list will prove of interest and use to other workers. Families, genera and species are arranged alphabetically.

The writer wishes to express his thanks to the specialists of the Imperial Institute of Entomology, the Department of Entomology of the British Museum, and others who identified the insects concerned, and to Mr. F. C. Deighton, Plant Pathologist, for naming the plants.

COLEOPTERA.

ANTHRIBIDAE.

Araecerus fasciculatus, de Geer	Avocado (*Persea gratissima*) (fruit), *Caesalpinia pulcherrima* (seed), cassava (*Manihot utilissima*) (stem), coffee (berries), *Cola nitida* (fruit), maize (ears), *Morinda geminata* (fruit).
Gynandrocerus praecox, Klb.	Oil palm (*Elaeis guineensis*).
Phloeobius humilis, Klb.	*Bauhinia* sp.
Zygaenodes monstrosus, Pasc.	Cotton.

BOSTRYCHIDAE.

Apate monachus, F.	*Aleurites montana*, avocado, cassava, *Cola*, guava, *Peltophorum africanum*.
Micrapate neglecta, Lesne	Avocado (twigs), cotton (stem).
Xyloperthodes nitidipennis, Murr.	*Poinciana* sp., *Ficus capensis*.
Xylopsocus capucinus, F.	Cotton (stem), *Aleurites montana*.

BRENTHIDAE.

Cerobates conveniens, Kln.	Diseased rubber (*Hevea*) tree.
Jonthocerus conradti, Senna	Oil palm (trunk).

BRUCHIDAE.

Bruchus marshalli, Pic. var.	*Phaseolus* and *Vigna* pods.
Pachymerus cassiae, Gyll.	*Cassia alata*, *C. sieberiana* and *Hibiscus sabdariffa* ; pods.
Spermophagus latithorax, Boh.	*Eugenia jambos* (flowers).

CASSIDIDAE.

Acrocassis conducta, Boh.	*Ipomoea batatas*, *Ipomoea* sp.
epipleuralis, Wse.	*Ipomoea batatas*.
roseomarginata, Boh.	*Ipomoea batatas*.
Aspidomorpha afzelii, Boh.	*Ipomoea batatas*.
dissentanea, Boh.	*Ipomoea* spp.
obovata, Klug	Oil palm.
togata, Thoms.	*Ipomoea batatas*.

CERAMBYCIDAE.	
Mecaspis atripennis, Hope	Avocado (flowers).
CETONIIDAE.	
Clastocnemis maculatus, Burm.	Oil palm (male inflorescence, decaying petiole).
Diplognatha gagates, Forst.	Cotton and other flowers, soft fruits.
Myoderma alutacea, Schönh.	Oil palm (male inflorescence).
Pachnoda cordata, Drury	Coconut, various flowers and soft fruits.
marginata, Drury	Various flowers and soft fruits.
marginella, F.	Cashew (*Anacardium occidentale*) (leaves).
Platygenia barbata, Schönh.	Oil palm (male inflorescence).
Stephanorrhina guttata, Oliv.	Banana.
CLERIDAE.	
Cylidrus fasciatus, Cast.	*Poinciana* sp.
CLYTRIDAE.	
Labidognatha coerulans, F.	*Hibiscus esculentus* (flowers).
COCCINELLIDAE.	
Epilachna chrysomelina, F.	Cucurbits.
deleta, Muls.	*Solanum melongena* and *S. anomalum*.
similis, Thunb. var. *assimilis*, Muls.	Maize, millet, rice, other grasses, cotton.
CRYPTOCEPHALIDAE.	
Cryptocephalus löwii, Suff.	*Zinnia* (flowers).
obesus, Suff.	*Arachis hypogaea*, grasses.
w-nigrum, Suff.	*Arachis hypogaea*, rose.
CUCUJIDAE.	
Silvanus advena, Waltl	Banana (fruit).
CURCULIONIDAE.	
Alcides dentipes, Ol.	*Ipomoea* spp.
senex, Sahlb.	*Citrus*.
Aorus spadiceus, Gyll.	*Corchorus olitorius*, grasses, ginger, rice, millet (leaf, inflorescence, ears).
Apoderus testaceus, Voss	*Pterocarpus indicus*.
fuscicornis, Boh.	*Combretum comosum*, rose.
Balanogastris colae, Desbr.	*Cola nitida* and *C. lateritia* (fruit).
Calandra oryzae, L.	Rice (ears).
Cosmopolites sordidus, Germ.	*Musa* spp.
Cylas brunneus, F.	*Ipomoea batatas*, *I. digitata*.
puncticollis, Boh.	*Ipomoea batatas*.
Cyllophorus fasciatus, Fst.	*Pterocarpus indicus*.

CURCULIONIDAE—*cont.*

Derelomus kamerunicus, Fst.	Oil palm (male inflorescence).
plagiatus, Fst.	Oil palm (male inflorescence).
subvittatus, Fst.	Oil palm (male inflorescence).
Leurostenus elaeidis, Mshl.	*Hibiscus sabdariffa.*
Lixus rhomboidalis, Boh.	*Amarantus caudatus* (leaves, root and stalk borer).
Paremydica insperata, Fst.	*Cola nitida* (fruit).
Rhina afzelii, Fhs.	Oil and coconut palms.
Rhynchophorus quadrangulus, Qued.	Oil palm.
phoenicis, F.	Oil palm.
Temnoschoita quadripustulata, F.	Oil palm (trunk and fruit head).

DYNASTIDAE.

Archon centaurus, Burm.	Coconut and oil palms.
Heteroligus claudius, Klug	
Oryctes boas, F.	Coconut and oil palms.
erebus, Burm.	Coconut and oil palms.
owariensis, P. de B.	Coconut and oil palms.

ENDOMYCHIDAE.

Stenotarsus guineensis, Gerst.	Palm.

EUMOLPIDAE.

Casmena murrayi, Chap.	Palm.
Menius fulvicornis, Jac.	*Nicotiana* sp.
semipiceus, Jac.	Palm.
Syagrus calcaratus, F.	Cotton.
puncticollis, Bry.	Oil palm.

GALERUCIDAE.

Asbecesta cyanipennis, Har.	Cucumber.
Buphonella africana, Jac.	*Arachis*, rice.
metallica, Jac.	*Arachis.*
Hyperacantha bidentata, F.	Pumpkin.
kraatzi, Jac.	Cucumber.
Leptaulaca deleta, Sahlb.	Rice.
Megaleruca griseosericans, Thoms.	*Canna*, *Trema guineensis* (larval host).
Monolepta dalmani, Jac.	*Vigna sinensis.*
duplicata, Sahlb.	Palm.
fulvosignata, Jac.	Palm.
intermedia, Rits.	Palm.
limbata, Ol.	Oil palm.
lineata, Karsch	*Phaseolus vulgaris*, *Sorghum vulgare.*
tenuicornis, Jac.	Coconut palm, *Vigna sinensis*, rice (inflorescence).
versicolora, Wse.	*Artocarpus integrifolia.*
Ootheca mutabilis, Sahlb.	Avocado, *Phaseolus vulgaris*, Cucurbits.
Platyxantha discoidalis, Jac.	*Artocarpus integrifolia.*

HALTICIDAE.	
Aphthona guavae, Bry.	Guava.
sierraleonis, Bry.	*Arachis.*
Cercyonia citri, Bry.	Lime and lemon; shoot borer and defoliator.
Chaetocnema zeae, Bry.	*Arachis*, maize, millet, rice, and other grasses, ginger.
Decaria abdominalis, Jac.	*Cola nitida* (flowers).
Podagrica apicalis, Jac.	*Arachis.*
dilecta, Dalm.	*Arachis*, cotton, *Hibiscus* spp., *Sorghum vulgare.*
spadicea, Dalm.	Avocado, *Vitis vinifera*, grasses, *Hibiscus* spp., *Cola.*
uniforma, Jac.	Cotton, *Hibiscus* spp.
HISPIDAE.	
Agonia 4-punctata, Guér.	Grasses (*Sorghum*, etc.).
Chrysispa paucispina, Wse.	Rice and other grasses.
Coeloenomenodera elaeidis, Maulik.	Coconut and oil palms.
Dorcathispa bellicosa, Guér.	Maize, *Sorghum vulgare*, and other grasses.
Oncocephala proxima, Gestro	Grasses, *Ipomoea* sp.
HISTERIDAE.	
Apobletes angolensis, Lew.	*Cola* fruit.
Hololepta semicincta, Mars.	Coconut palm (trunk).
Teretriosoma afrum, Lewis	*Poinciana* sp.
HYDROPHILIDAE.	
Dactylosternum abdominale, F.	Dead coconut.
LAGRIIDAE.	
Lagria cuprina, Thoms.	*Cola nitida*, and general.
guineensis, Borch.	General.
viridipennis, F.	*Phaseolus vulgaris*, and general.
LAMIIDAE.	
Bixadus sierricola, White	Coffee.
Diastocera trifasciata, F.	General girdler.
Ecphora testator, F.	*Mitragyna stipulosa.*
Glenea giraffa, Dalm.	*Cola nitida* (branch borer).
Hecyrida obscurator, F.	Banana (defoliator).
Homelix cribratipennis, Thoms.	Cacao (girdler).
Moecha adusta, Har.	Cacao (girdler).
Monohammus ruspator, F.	Cassava (borer).
Phryneta aurocincta, Guér.	General girdler.

LUCANIDAE.	
Metopodontus antilope, Swed.	*Poinciana* sp. (girdler).
senegalensis, Cast.	*Poinciana* sp. (girdler).
LYCIDAE.	
Lycus sinuatus, Schönh.	*Cola nitida*.
MELOIDAE.	
Decapotoma affinis, Ol.	*Arachis* (flowers).
Epicauta oculata, F.	General.
Mylabris seminigra, Voigts	*Cola nitida*.
MELOLONTHIDAE.	
Trochalus carinatus, Schönh.	Avocado.
gibbus, F.	Avocado, *Cola nitida*, cotton.
pilula, Klug	Avocado, *Cola nitida*.
MELYRIDAE.	
Hapalochrus azureus, Er.	*Arachis*.
inchoatus, Champ.	Oil palm.
NITIDULIDAE.	
Axyra elongata, Murr.	*Carica papaya* (fruit), oil palm (trunk).
Brachypeplus pilosellus, Murr.	Avocado (fruit), banana and oil palm (inflorescences), maize (ears).
Carpophilus binotatus, Murr.	Cashew (fruit), *Sorghum vulgare*.
dimidiatus, F.	*Cola nitida* (fruit), maize (ears).
Cryptarcha senegalensis, Reitt.	Mango (fruit).
Microporum congolense, Grouv.	Oil palm (male infloresence).
PLATYPIDAE.	
Platypus hintzi, Schauf.	Beneath bark of dead *Hevea*.
RUTELIDAE.	
Adoretus similis, Bend.	Cashew.
Anomala chalcophora, var. *minor*, Ohs.	Cashew.
denuda, Arr.	Avocado, *Cola nitida*, guava.
Chaetadoretus setipennis, Ohs.	Avocado, guava, rose.
Popillia obliterata, Gyll.	Rose.
viridissima, Blanch.	*Bauhinia* sp.
SCOLYTIDAE.	
Coccotrypes ghesquieri, Egg.	Palm kernels.
perditor, Bldf.	Oil palm (nuts).
pygmaeus, Eich.	Oil palm (nuts).
Poecilipes sierraleonensis, Eggers.	*Poinciana* (pod).
Premnobius ambitiosus, Schauf.	Furniture.
Stephanoderes attenuatus, Eggers	*Cola nitida* (branches).
polyphagus, Eggers	*Phaseolus vulgaris* (stem).
stuhlmanni, Hag.	Coffee (stem-borer).

SCOLYTIDAE—*cont.*	
Xyleborus compactus, Eich.	Cacao and coffee (stem-borer).
confusus, Eich.	*Carica papaya.*
morstatti, Haged.	Coffee, *Bauhinia* sp.
perforans, Woll.	Palm (trunk).
TELEPHORIDAE.	
Malthodes pilosicornis, Pic.	Oil palm.
TENEBRIONIDAE.	
Perichilus brevicornis, Qued.	Pineapple.
TROGOSITIDAE.	
Gymnochila squamosa, Murr.	*Poinciana* spp.

DERMAPTERA.

FORFICULIDAE.	
Diaperasticus erythrocephalus, Ol.	Guinea corn (*Sorghum vulgare*) and maize (ears and leaves), rice (flowers and ears).

DIPTERA.

ANTHOMYIIDAE.	
Atherigona excisa, Thoms.	Avocado (fruit), maize (ears), melon (fruit) tomato (fruit).
LONCHAEIDAE.	
Lonchaea aurea, Macq.	Tomato (fruit).
plumosissima, Bezzi	Tomato (fruit).
SYRPHIDAE.	
Eumerus obliquus, F.	Tomato (fruit).
TRYPETIDAE.	
Ceratitis colae, Silv.	*Cola nitida* (fruit).
giffardi, Bez.	*Sarcocephalus esculentus, S. diderrichii,* de Wild.
punctata, Wd.	*Chrysophyllum pruniforme, Conopharyngia longiflora.*
Dacus bivitattus, Big.	*Carica papaya*, Cucurbits, tomato.
punctatifrons, Karsch	Cucurbits, tomato.
vertebratus, Bez.	Tomato.
momordicae, Bez.	Cucurbits.
Tririthrum coffeae, Bez.	Coffee.
APIDAE.	
Ceratina viridissima, D. T.	Cassava.
Xylocopa africana, F.	Lime (*Citrus medica*, var. *acida*).
albiceps, F.	Lime (*Citrus medica*, var. *acida*).
imitator, Sm.	Lime (*Citrus medica*, var. *acida*).
obscurata, Sm.	Lime (*Citrus medica*, var. *acida*).
olivacea, F.	Lime (*Citrus medica*, var. *acida*).
torrida, West.	*Cola nitida.*
varipes, Sm.	Lime.

LEPIDOPTERA (Rhopalocera).

LYCAENIDAE.	
Euchrysops malathana, Boisd.	*Phaseolus vulgaris, Vigna sinensis.*
Lycaenesthes larydas, Cram.	*Cassia podocarpa.*
Deudorix bimaculata, Hew.	Coffee (berries), *Heinsia pulchella* (fruit).
NYMPHALIDAE.	
Hypolimnas dubia, Pal.	*Citrus* spp.
PAPILIONIDAE.	
Papilio dardanus, F.	*Citrus.*
demodocus, Esp.	*Citrus.*
nireus, L.	*Citrus.*
PIERIDAE.	
Catopsilia florella, F.	*Cassia podocarpa, C. javanica.*

LEPIDOPTERA (Heterocera).

ARCTIIDAE.	
Diacrisia maculosa, Cram.	*Arachis hypogaea, Hippeastrum equestre.*
occidens, Roths.	*Arachis hypogaea.*
rattrayi, Roths.	*Combretum* sp., *Hippeastrum equestre, Zephyranthes tubispatha.*
CHARIDEIDAE.	
Ninia plumipes, Drury	*Cola nitida* (leaf roller).
COSMOPTERYGIDAE.	
Pyroderces coriacella, Snell.	Banana (fruit), maize (ears).
COSSIDAE.	
Engyophlebus obesus, Karsch	Cacao and *Cola nitida.*
Xyleutes armstrongi, Hmps.	Coffee, *Psidium guajava.*
EUCOSMIDAE.	
Argyroploce colivora, Meyr.	*Cola nitida* (fruit).
leucotreta, Meyr.	Avocado (fruit), *Eugenia uniflora*, grapefruit, guava (fruit), maize (ear).
wahlbergiana, Zell.	*Ricinus communis* (inflorescence).
GELECHIIDAE.	
Brachyacma palpigera, Wals.	*Bauhinia* sp. (pod).
Sitotroga cerealella, Ol.	Maize (ears), rice.
GEOMETRIDAE.	
Xenimpia trizonata erosa, Warr.	*Ricinus communis.*
GRACILARIIDAE.	
Acrocercops bifasciata, Wals.	Cotton.
caerulea, Meyr.	*Phaseolus vulgaris, Pueraria, Vigna sinensis.*
hexalocha, Meyr.	*Citrus.*
siphonaula, Meyr.	*Cola.*

LASIOCAMPIDAE.	
Andraphisia subfascia, Wlk.	*Citrus*, cassava, *Cassia*.
Catalebeda producta, Wlk.	*Pterocarpus indicus*.
LIMACODIDAE.	
Ctenocompa hilda, Druce	*Voandzeia subterranea*.
Parasa vivida, Wlk.	Coffee, *Sarcocephalus esculentus*.
LYMANTRIIDAE.	
Dasychira basalis, Wlk.	*Arachis*.
rhabdota, Collnt.	*Cola nitida*.
LYONETIIDAE.	
Plemyristis oenochares, Meyr.	*Bauhinia* sp. (pod).
NOCTUIDAE.	
Achaea albicilia, Butl. *	
albifimbria, Wlk.	
boris, Geyer *	
catella, Guen.*	
catocaloides, Guen.*	*Alchornia cordifolia, A. hirtella, Byrsocarpus coccineus, Cnestis ferruginea, Cola nitida, Combretum comosum, Connarus africanus, Costus afer, Dichapetalum toxicarium, Dioscorea hirtiflora, Leptoderris* sp., *Macaranga huraefolia, Millettia Barteri, Napoleona Heudelotii, Ochthocosmus africanus, Phyllanthus discoideus, Sorindeia juglandifolia, Uvaria chamae.*
dasybasis, Hmps.*	
ezea, Cram.*	*Combretum comosum, C. mucronatum, Ochthocosmus africanus.*
faber, Holl.*	*Combretum comosum, Ochthocosmus africanus.*
finita, Guen.*	
hieroglyphigera, Strand *	
indicabilis, Wlk.*	
lienardi, Boisd.*	*Combretum comosum, C. mucronatum, Napoleona Heudelotii, Ochthocosmus africanus, Phyllanthus discoideus.*
mercatoria, F.*	
mormoides, Wlk.*	
trapeziodes, Guen.*	*Ochthocosmus africanus, Phyllanthus discoideus.*
Anomis auragoides, Guen.	*Hibiscus.*

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* = Adult is a fruit-piercer (*Citrus*, mango, cashew).

NOCTUIDAE—*cont.*

Anua david, Holl.*	*Combretum comosum.*
dilecta, Wlk.*	
mejanesi, Guen.*	*Combretum comosum.*
producta, Holl.*	
selenaris, Guen.*	
tirhaca, Cram.*	
Brithys pancratii, Wlk.	*Hippeastrum equestre* (all parts of plant), *Hymenocallis littoralis*, *Zephyranthes tubispatha.*
Busseola fusca, Hmps.	Maize (borer).
Catephia iridocosma, B. Bkr.	*Ipomoea batatas.*
Characoma stictigrapta, Hmps.	Cacao (fruit), *Cola nitida* (fruit, leaf, and flower-buds).
Cocytodes inaura, Holl.*	
Earias biplaga, Wlk.	*Hibiscus rosa-sinensis*, *H. sabdariffa*, *H. sterculiifolius.*
citrina, Saalm.	*H. sabdariffa.*
Episparis penetrata, Wlk.	*Sarcocephalus esculentus.*
Heliophisma catocalina, Holl.*	
klugi, Boisd.*	
croceipennis, Wlk.*	
Heliothis armigera, Hbn.	Tomato (stem and fruit).
Hypocala rostrata, F.*	
subsatura, Guen.*	
Lacera alope, Stoll *	
Lagoptera occidens, Hmps.*	
Leucinodes orbonalis, Guen.	Tomato (fruit), *Solanum macrocarpum* (fruit).
Lophocrama phoenicochlora, Hmps.	*Cola nitida* (leaf roller).
Mocis undata, F.	*Phaseolus* or *Vigna* sp., *Pterocarpus indicus.*
Othreis divitiosa, Wlk.*	*Dioscoreophyllum tenerum*, *Rhigiocarya racemifera.*
fullonica, L.*	*Dioscoreophyllum tenerum*, *Stephania Dinklagei*, *Synclisia ferruginea*, *Tiliacora* sp. near *Dinklagei*, *Triclisia patens.*
materna, L.*	*Rhigiocarya racemifera.*
Plusia acuta, Wlk.	Banana, *Nicotiana* sp., *Rhigiocarya racemifera.*
chalcites, Esp.	Cacao, *Nicotiana* sp.
signata, Fabr.	Cacao, *Calendula officinale*, *Cineraria.*

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*=Adult is a fruit-piercer (*Citrus*, mango, cashew).

Noctuidae.—*cont.*	
Prodenia litura, Fab.	*Arachis* (stem-borer, flowers), *Hippeastrum equestre*, *Hymenocallis littoralis*, *Phaseolus lunatus*, *Synedrella nodiflora*, tomato (fruit), *Vigna sinensis*.
Pseudololna eximia, Holl.*	
Serrodes partita, F.*	*Deinbollia pinnata*.
trispila, Mab.*	*Lecaniodiscus cupanioides*.
Sphingomorpha chlorea, Cram.*	
pudens, Holl.*	
Spodoptera mauritia, Boisd.	Sabal palm.
Tolna versicolor, Wlk.*	
Notodontidae.	
Stauropus varia, Walk.	*Psidium guajava*.
Pyralidae.	
Lamprosema indicata, F.	*Arachis*.
Margaronia indica, Saund.	Cucumber.
Maruca testulalis, Hb.	*Poinciana* sp. (pods), *Phaseolus vulgaris* (pods).
Sylepta balteata, F.	*Anacardium occidentalis*.
derogata, F.	Cotton, *Hibiscus esculentus*.
polycymalis, Hmps.	*Cola nitida*.
semifugens, Hmps.	*Cola nitida* (leaf-sewer).
Saturniidae.	
Cyrtogone herilla, Westw.	Cashew, *Sorindeia juglandifolia*.
Sphingidae.	
Acherontia atropos, L.	*Clerodendron paniculatum*, *Ipomoea batatas*, *Jasminum pubescens*, *Solanum duplosinuatum*, *S. melongena*, *Vigna sinensis*.
Cephonodes hylas, L.	*Coffea*.
Deilephila nerii, L.	*Rauwolfia vomitoria*, *Sarcocephalus esculentus*, *Tabernaemontana coronaria*.
Herse convolvuli, L.	*Heinsia pulchella*, *Ipomoea batatas*, *I. digitata*.
Polyptychus carteri, Butl.	*Cola nitida*.

ORTHOPTERA.

Acrididae.	
Locusta migratoria migratorioides, R. & F.	Palms (coconut and Sabal), pineapple, rice, maize, and other grasses.
Schistocerca gregaria, Forsk.	Various ; of unusual occurrence.
Zonocerus variegatus, L.	General.

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*=Adult is a fruit-piercer (*Citrus*, mango, cashew).

BLATTIDAE.	
Periplaneta australasiae, L.	Omnivorous.
Theganopteryx senegalensis, F.	Omnivorous.
GRYLLIDAE.	
Brachytrypes membranaceus, Dru.	General.
Gryllotalpa africana, P. B.	General.
Gryllus lucens, Wlk.	General.
Gymnogryllus miurus, Sauss.	General.
Scapsipedus marginatus, Afz.	General.

RHYNCHOTA.

ALEURODIDAE.	
Aleuromarginatus tephrosiae, Corbett	*Tephrosa candida*, *T. Vogelii.*
Neomaskellia bergi, Mask.	Grasses.
APHIDIDAE.	
Aphis laburni, Kalt.	*Arachis hypogaea*, *Vigna sinensis.*
sorghi, Theob.	*Sorghum vulgare.*
Cerataphis lataniae, Boisd.	Palms.
Doralis medicaginis, Koch.	*Arachis*, *Gliricidia maculata.*
Pentalonia nigronervosa, Coq.	*Musa* spp.
Toxoptera aurantii, Boyer	*Bauhinia* sp.
CAPSIDAE.	
Engytatus volucer, Kirk.	*Nicotiana* sp.
Halticus tibialis, Reut.	*Arachis* (nymphal host), grasses; *Physalis peruviana*, *Vigna sinensis* (nymphal host).
Prodromus aethiopicus, Popp.	*Arachis*, oil palm.
Sahlbergella singularis, Hgl.	*Berria ammonilla.*
Torma colae, China	*Cola nitida* (flowers).
Proboscidocoris punctaticollis, Reut.	*Thunbergia* sp. (flowers).
CERCOPIDAE.	
Locris maculata, F.	Sugar-cane, maize, and other grasses.
Triecphora karschi, Dist.	Palms.
CIXIIDAE.	
Nisia atrovenosa, Wlk.	*Vigna sinensis*, rice, millet.
COCCIDAE.	
Aspidiotus cyanophylli, Sign.	Oil palm.
destructor, Sign.	*Anona muricata*, *A. squamosa*, *Artocarpus incisa*, avocado, banana, *Carica papaya*, coconut, *Dioscorea esculenta*, mango, oil palm, *Piper umbellatum*, *Plumeria*, *Sarcocephalus esculentus*, *Xanthosoma sagittifolium.*

COCCIDAE—*cont.*

Aspidiotus—*cont.*

elaeidis, March.	Banana, coconut, oil palm.
gowdeyi, Newst.	Coconut.
harti, Ckll.	*Zingiber officinale.*
lataniae, Sign.	Oil palm.
sacchari, Ckll.	Coconut, grass (roots).
Ceronema africana, Macf.	*Arachis*, *Cajanus indicus.*
Ceroplastodes ? *ritchiei*, Laing	*Anona muricata.*
Chionaspis ritchiei, Laing	Coffee.
Chrysomphalus rossi, Mask.	Oil palm, *Achras sapota.*
rossi, var. *colae*, Lg.	*Cola nitida.*
Coccus probably *viridis*, Green	*Plumeria.*
Ctenochiton arborescens, Laing	Coconut.
Diaspis boisduvalii, Sign.	Pineapple.
lutea, Newst.	Oil palm.
Ferrisiana virgata, Ckll.	*Arachis*, avocado, *Bauhinia* spp., calabash (*Crescentia*), *Calopogonium mucunoides*, cassava, *Cassia sieberiana*, *Clerodendron paniculatum*, coffee, *Gliricidia maculata*, guava, *Jatropha* spp., *Tecoma stans*, tomato, *Waltheria lanceolata.*
Lepidosaphes beckii, Newm.	*Citrus.*
Leucaspis cockerelli, de Charm.	Oil palm.
Phenacaspis sp.	Oil palm.
Phenacoccus phaseoli, Laing	*Phaseolus vulgaris.*
Pinnaspis aspidistrae, Sign.	Oil palm.
buxi, Bché.	Coconut.
Prontaspis citri, Comst.	*Citrus.*
Pseudaonidia baikeae, Newst.	*Cola nitida.*
trilobitiformis, Green	*Citrus*, coffee, guava, *Nerium oleander.*
Pseudococcus brevipes, Ckll.	*Canna indica* (roots), oil palm, pineapple, *Sporobolus pyramidalis* (roots).
brevipes, Ckll. var.	*Vigna sinensis* (roots).
near *comstocki*, Kuw.	*Phaseolus vulgaris* (roots).
citri, Risso	*Anisophyllea laurina.*
njalensis, Laing	Coffee (including berries), *Piper umbellatum.*
Pseudoparlatoria ostreata, Ckll.	*Carica papaya.*
Saissetia nigra, Nietn.	Coffee, guava, *Plumeria.*
subhirsuta, Newst.	*Cola nitida.*
Selenaspidus articulatus, Morg.	Coconut, grapefruit (fruit).
kamerunicus, Ldgr.	Coconut.
spinosus, Laing	Banana.

COCCIDAE—*cont.*	
Stictococcus intermedius, Newst.	*Cola nitida* and *C. lateritia.*
multispinosus, Newst.	*Cassia* sp. *Cola nitida* (fruit).
sjöstedti, Ckll.	*Cola nitida.*
COREIDAE.	
Leptocorisa apicalis, Westw.	Rice and other grasses, groundnut.
Liorhyssus hyalinus, F.	Lettuce (inflorescence and seeds).
Mirperus torridus, Westw.	Rice, *Zinnia* (flowers).
Riptortus tenuicornis, Dall.	*Citrus*, rice.
DELPHACIDAE.	
Peregrinus maidis, Ashm.	Maize, rice, and other grasses.
DERBIDAE.	
Cedusa aburiensis, Muir	Oil palm.
nigripes, Muir	*Raphia vinifera.*
Diostrombus dilatatus, West.	Banana, coconut, oil palm, Sabal palm, sugar cane.
cocos, Muir	Coconut, oil palm.
grahami, Dist.	Oil palm.
luteus, Muir	Coconut palm, oil palm, Sabal palm.
nitidus, Muir	Coconut, oil palm, rice, Sabal palm.
Helcita occidentalis, Muir	Oil palm.
Kamendaka albomaculata, Muir	Coconut, fern, guava, maize, oil palm, *Pandanus* sp.
Levu africana, Muir	Oil palm.
Lydda annetti, Muir	Oil palm, *Pandanus* sp.
cocos, Muir	Coconut.
elaeidis, Muir	Oil palm.
hargreavesi, Muir	Oil palm.
lineatipes, Muir	Oil palm.
Mysidioides africana, Muir	Oil palm.
Paraphenice neavei, Muir	*Abroma augusta, Hibiscus esculentus.*
sierraleonensis, Muir	Oil palm.
Patara elaeidis, Muir	Oil palm.
hargreavesi, Muir	Oil palm.
Phenice stellulata, Boh.	Oil palm.
Proutista fritillaris, Boh.	Coconut, guava, oil palm, Sabal palm, sugar-cane and other grasses.
Zoraida aburiensis, Muir	Oil palm.
bohemani, Westw.	Oil palm.
maculicosta, Muir	Sabal palm.
sinuosa, Boh.	Oil palm.

FULGORIDAE.	
Pyrops tenebrosus, F.	Beans, rice, tomato.
LOPHOPIDAE.	
Elasmoscelis trimaculata, Wlk.	Sugar-cane and other grasses.
LYGAEIDAE.	
Graptostethus servus, F.	*Canavalia ensiformis*, *Sorghum vulgare*.
Lygaeus festivus, Thnbg.	*Hibiscus esculentus*, *Nicotiana* sp.
furcatus, F.	*Gloriosa superba* (flowers and seeds).
Oxycarenus fieberi, St.	*Cola nitida*, *Hibiscus* spp.
gossypinus, Dist.	*Hibiscus* spp.
MEENOPLIDAE.	
Anigrus stramineus, Muir	Oil palm.
Inxwala bergrothi, Muir	Oil palm.
Kermesia albipennis, Muir	Oil palm.
MEMBRACIDAE.	
Anchon senegalensis, Fairm.	*Petraea volubilis*.
Gargara addahensis, Dist.	*Bauhinia* sp., *Combretum comosum*.
PENTATOMIDAE.	
Afrius purpureus, Westw.	Cassava.
Aspavia armigera, F.	Rice (ears).
Aspongopus nigroviolaceus, P. B.	Beans.
Brachyplatys aethiops, Dall.	Maize.
testudo-nigra, Deg.	*Arachis*.
PLATASPIDAE.	
Coptosoma falloui, Mont.	*Mucuna*, *Sorghum vulgare*.
marginella, Dall.	*Arachis*, *Crotalaria juncea*, *Phaseolus vulgaris*, *Vigna sinensis*.
PSYLLIDAE.	
Mesohomotoma tessmanni, Aulm.	Cacao, *Cola nitida*.
Phytolyma lata, Wlk.	*Chlorophora excelsa*.
PYRRHOCORIDAE.	
Dysdercus fasciatus, Sign.	Cotton.
melanoderes, Karsch	Cotton.
migratorius, Dist.	Oil palm.
superstitiosus, F.	Cotton, *Hibiscus esculentus*.
RICANIIDAE.	
Ricanopsis semihyalina, Mel.	*Cola nitida* (nymphal host).
TINGIDAE.	
Cantacader tenuipes, St.	Grasses, guava.
TROPIDUCHIDAE.	
Numicia taenia, F.	Oil palm.

THYSANOPTERA.

Bactridothrips laingi, Bagn.	Cacao, *Mitragyna stipulosa*.
Bolothrips marshalli, Pries.	*Bauhinia* sp., cassava, *Lochnera rosea*.
Brachyurothrips hargreavesi, Bagn. ...	*Hydrangea*, *Punica granatum*, *Solanum melongena*, tomato.
Eurhynchothrips flavicornis, Bagn. ...	*Mitragyna stipulosa*.
Heliothrips haemorrhoidalis, Bch. var. *angustior*, Priesner	*Codiaeum variegatum*, *Punica granatum*.
Hercothrips femoralis, Reut.	*Arachis*.
Hoplandothrips hystrix, Bagn.	*Citrus decumana*.
Machatothrips braueri, Karny	Coffee (base of berry-stalks), cassava (inside stem).
multidens, Bagn. ...	Coffee, ex borer tunnels.
paucidens, Bagn. var. *bicolorisetosus*, Bagn.	Coffee, ex borer tunnels.
Selenothrips hargreavesi, Bagn. ...	*Acalypha*.
rubrocinctus, Giard ...	Avocado.
Taeniothrips ventralis, Hood	Tomato.
Thrips exilicornis, Hood	*Agelaea nitida*, banana, *Citrus* (flowers).
Zeugmatothripoides africanus, Bagn. ...	*Cola nitida*.

Insects Affecting stored products, etc.

COLEOPTERA.

ANOBIIDAE.

Lasioderma serricorne, F.	Books, ginger, pigeon-pea.
Sitodrepa panicea, L.	*Tropaeolum* (seeds).

ANTHRIBIDAE.

Araecerus fasciculatus, de Geer	Coffee, Cola nuts, ginger, maize, tobacco, turmeric.

BOSTRYCHIDAE.

Rhizopertha dominica, F.	Ginger, maize, rice.

BRUCHIDAE.

Bruchus analis, F.	Beans, peas.
impressithorax, Pic	Legumes.
marshalli, Pic	Beans, cowpeas.
obsoletus, Say	*Phaseolus*.
ornatus, Boh.	*Vigna sinensis*.
rhodesianus, Pic	Cowpeas.
Pachymerus cassiae, Gyll.	*Cassia* spp.

CLERIDAE.

Necrobia rufipes, de Geer	Palm kernels.

CUCUJIDAE.	
Ahasverus advena, Waltl.	Rice.
Laemophloeus pusillus, Schönh.	Palm kernels, rice.
Oryzaephilus surinamensis, L.	Ginger, maize, sugar.
CURCULIONIDAE.	
Balanogastris colae, Desbr.	Cola nuts.
Calandra oryzae, L.	Maize, peas, rice.
Paremydica insperata, Fst.	Cola nuts.
NITIDULIDAE.	
Brachypeplus pilosellus, Murr.	Maize.
Carpophilus dimidiatus, F.	Cola nuts, maize, rice.
SCOLYTIDAE.	
Coccotrypes perditor, Bldf.	Palm kernels.
pygmaeus, Eich.	Palm kernels.
TENEBRIONIDAE.	
Tribolium castaneum, Hbst.	Flour, ground-nuts, pigeon-pea, rice.
TROGOSITIDAE.	
Tenebroides mauritanicus, L.	Groundnuts, rice.

LEPIDOPTERA.

BLASTOBASIDAE.	
Blastobasis byrsodepta, Meyr.	Ginger, Cola nuts.
GELECHIIDAE.	
Sitotroga cerealella, Ol.	Maize, rice.
NOCTUIDAE.	
Characoma stictigrapta, Hmps.	Cola nuts.
PYRALIDAE.	
Achroia grisella, Fab.	Rice.
Corcyra cephalonica, Stn.	Groundnut, pigeon pea.
TINEIDAE.	
Setomorpha rutella, Z.	Rice.

RHYNCHOTA.

COCCIDAE.	
Aspidiotus harti, Ckll.	Ginger, Yams.
Pseudococcus sp.	Yams.

THYSANURA.

Acrotelsa collaris, F.	Clothes, paper, books.

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st April and 30th June, 1937 :—

Mr. W. Allan, Entomologist :—8 Coleoptera and 30 early stages ; from Northern Rhodesia.

Dr. H. F. Barnes, Rothamsted Experiment Station :—25 Parasitic Hymenoptera ; from England.

Dr. H. Blunck :—6 Parasitic Hymenoptera ; from Germany.

Dr. G. Bondar :—72 Coleoptera ; from Brazil.

Mr. H. Britten, Manchester Museum :—53 Parasitic Hymenoptera and 15 cocoons ; from England.

Mr. L. L. Buchanan :—2 Coleoptera ; from the United States of America.

Prof. P. A. Buxton, London School of Hygiene & Tropical Medicine :—2 *Chrysops* ; from the Cameroons.

Mr. L. Cheng :—11 Coleoptera, 2 Parasitic Hymenoptera, 6 Lepidoptera, 1 species of Aphidae, and 100 other Rhynchota ; from China.

Dr. A. Chiaromonte :—3 Noctuid larvae ; from Italian East Africa.

Chief Entomologist, Pretoria :—22 Coleoptera and 90 Parasitic Hymenoptera ; from South Africa.

Mr. J. T. Chu :—6 Lepidoptera ; from China.

Civil Veterinary Directorate, Baghdad :—60 Anoplura ; from Iraq.

Mr. L. D. Cleare, Junr., Government Entomologist :—4 Diptera, 15 Coleoptera, and 6 Lepidoptera ; from British Guiana.

Father P. A. Conrads :—22 Curculionidae ; from Tanganyika Territory.

Mr. G. H. Corbett, Government Entomologist :—2 Siphonaptera, 74 Diptera and 8 pupa-cases, 140 Coleoptera, 326 Parasitic Hymenoptera and 7 cocoons, 101 other Hymenoptera, 294 Lepidoptera and 100 pupa-cases, 80 Isoptera, 50 Rhynchota, 3 Orthoptera, 2 Planipennia, 3 Collembola, 25 Chelifera, 80 Snails and 6 Slugs ; from Malaya.

Coryndon Memorial Museum, Nairobi :—2 Nycteribiidae, 7 *Haematopota*, 3 Hippoboscidae, 222 other Diptera, 283 Coleoptera, 57 Parasitic Hymenoptera, 27 other Hymenoptera, and 8 Lepidoptera ; from East Africa.

Mr. A. Cuthbertson, Entomologist :—12 Diptera, 23 Coleoptera, 13 Parasitic Hymenoptera, 6 Lepidoptera, 6 Rhynchota, and 3 Mantispidae ; from Southern Rhodesia.

Dr. A. Da Costa Lima :—97 Coleoptera ; from Brazil.

Mr. R. C. M. Darling :—13 Diptera, 14 Coleoptera, 6 Hymenoptera, 9 Lepidoptera, and 183 Orthoptera ; from Arabia.

Mr. M. Delassus :—6 Parasitic Hymenoptera ; from Algeria.

Mrs. H. R. P. Dickson :—14 Coleoptera, 7 Hymenoptera, and 104 Orthoptera ; from Arabia.

Director of Agriculture, Borneo :—200 Rhynchota.

Director of Agriculture, Zanzibar :—43 Coleoptera and 5 early stages.

Director of Public Works, Lagos :—80 Formicidae and 800 Isoptera ; from Nigeria.

Mr. A. P. Dodd :—72 Coleoptera ; from Queensland.

Empire Cotton Growing Corporation :—3 Coleoptera ; from South Africa.

Mr. J. L. Froggatt, Government Entomologist :—30 Coleoptera, 5 Parasitic Hymenoptera, 6 other Hymenoptera, 38 Lepidoptera, 7 Rhynchota, and 12 Orthoptera ; from New Guinea.

Dr. L. Fulmek :—54 Parasitic Hymenoptera.

Mr. P. F. Garthwaite, Forest Entomologist :—49 Diptera and 18 pupa-cases, 59 Parasitic Hymenoptera, 121 Lepidoptera and 64 pupa-cases ; from Burma.

Mr. F. D. Golding, Government Entomologist :—8 Tabanidae, 9 *Glossina*, 16 other Diptera, 16 Coleoptera, 12 Lepidoptera, 25 Rhynchota, and 60 Orthoptera ; from Nigeria.

Government Entomologist, Coimbatore :—4 Coleoptera, 21 Lepidoptera, and 30 Rhynchota ; from South India.

Government Entomologist, Lyallpur :—1 Lamiid and 1 species of Fungus ; from the Punjab, India.

Mr. H. Hargreaves, Government Entomologist :—22 Diptera, 51 Coleoptera, 2 Parasitic Hymenoptera, 2 Tenthredinidae, 206 Lepidoptera, 42 Rhynchota, and 12 Psocidae ; from Uganda.

Mr. G. V. Hudson :—107 Coleoptera ; from New Zealand.

Imperial Chemical Industries, Ltd. :—1 species of Aphidae ; from England.

Imperial Entomologist, New Delhi :—9 Diptera, 150 Parasitic Hymenoptera, 18 Lepidoptera, and 2 Rhynchota ; from India.

Mr. H. B. Johnston :—600 Coleoptera, 300 Rhynchota, and 100 Psocidae ; from Uganda and the Sudan.

Mr. C. B. R. King :—8 Parasitic Hymenoptera, 50 Collembola, and 10 Mites ; from Ceylon.

Mr. C. D. Knight :—505 Coleoptera and 142 Rhynchota ; from Kenya Colony.

Mr. R. Korschefsky :—70 Curculionidae ; from Germany.

London Spinning Company, Ltd :—4 Coleoptera ; from England.

Mr. C. J. Louwerens :—173 Coleoptera ; from Java.

Mr. W. J. Lugard :—1 Pyrrhocorid ; from French Equatorial Africa.

Dr. J. W. Scott Macfie :—3 Diptera ; from Italy.

Mrs. K. C. Mackay :—1 Asilid and 4 Coleoptera ; from Ireland.

Mr. D. R. Mehta :—1 Pulicid ; from Kasauli, India.

Dr. D. Miller, Cawthron Institute :—8 Parasitic Hymenoptera and 4 Tenthredinidae ; from New Zealand.

Mr. J. Muggeridge, Government Entomologist :—2 slides of Coccidae and 2 other Rhynchota ; from New Zealand.

Mr. R. W. Mungomery :—18 Coleoptera and 50 early stages ; from North Queensland.

Musée Royal d'Histoire Naturelle, Bruxelles :—716 Coleoptera and 24 Parasitic Hymenoptera ; from Cyprus and Morocco.

Prof. R. Newstead, F.R.S. :—3 Tenthredinidae and 7 early stages ; from England.

Mr. C. Nicholson :—8 Parasitic Hymenoptera and 5 cocoons ; from England.

Mr. E. F. Peck, Veterinary and Agricultural Officer :—20 Tabanidae, 30 Dipterous early stages, 5 Lepidoptera, 5 Coleoptera and 3 larvae, and 200 Ticks ; from British Somaliland.

Messrs. Peek, Frean & Co., Ltd. :—31 Coleoptera ; from England.

Dr. S. V. P. Pill :—3 Coleoptera and 43 Orthoptera ; from South Iran.

Dr. H. Priesner :—5 Cecidomyiid early stages, 4 Coleoptera, and 300 Parasitic Hymenoptera ; from Egypt.

Mr. L. Pyenson :—4 Curculionidae ; from Brazil.

Mr. Y. R. Rao :—5 Orthoptera attacked by Mites ; from India.

Selangor Museum :—145 Coleoptera and 16 Parasitic Hymenoptera ; from Malaya.

Mr. F. A. Squire :—150 Parasitic Hymenoptera, 150 Formicidae, 150 Thysanoptera, 1 species of Coccidae, 2 species of Aphidae, and 12 Spiders ; from St. Vincent.

Mr. A. W. Stelfox :—21 Parasitic Hymenoptera and 30 cocoons ; from Ireland.

Mr. T. V. Subramanian, Entomologist :—4 Diptera, 26 Hymenoptera, 17 Lepidoptera, 1 species of Coccidae, and 8 Chelifera ; from Mysore, India.

Mr. J. Suire :—85 Parasitic Hymenoptera and 100 cocoons ; from France.

Mr. A. Théry :—154 Coleoptera ; from Gabon, West Africa.

Mrs. Thompson :—3 Diptera, 13 Coleoptera, and 4 Rhynchota ; from Tanganyika Territory.

Dr. W. H. Thorpe :—25 Parasitic Hymenoptera ; from England.

Dr. A. L. Tonnoir :—72 Parasitic Hymenoptera ; from Australia.

Dr. Ivar Trägårdh :—17 Parasitic Hymenoptera ; from Sweden.

Turkish Sugar Factory :—25 Coleoptera ; from Turkey.

Dr. F. van Emden :—60 Coleopterous early stages ; from New Guinea and Austria.

Mr. R. Veitch, Chief Entomologist :—164 Coleoptera ; from Queensland.

Mr. D. Vesey-Fitzgerald, Entomologist :—267 Coleoptera, 600 Parasitic Hymenoptera, and 1 species of Coccidae ; from East Africa.

Mr. J. Vinson :—17 Coleoptera ; from Mauritius.

West Java Experiment Station :—52 Coleoptera, 44 Lepidoptera, 1 species of Aphidae, 1 species of Psyllidae, and 20 other Rhynchota ; from Java.

Mr. F. G. S. Whitfield, Medical Entomologist :—10 Siphonaptera, 174 Culicidae, 196 other Diptera, 10 Coleoptera, 2 Hymenoptera, and 6 Lepidoptera ; from the Sudan.

Mr. H. Wilkinson, Entomologist :—2 Culicidae, 26 Tabanidae, 136 other Diptera, 71 Coleoptera and 126 early stages, 287 Parasitic Hymenoptera, 34 other Hymenoptera, 43 Lepidoptera, 100 Thysanoptera, 6 species of Coccidae, 1 species of Aleurodidae, 7 other Rhynchota, 13 Orthoptera, 2 Planipennia, 2 Ephemeridae, 25 Collembola, and 2 Spiders ; from Kenya Colony.

Mr. E. C. Zimmerman :—27 Coleoptera ; from Hawaii.

THE PREPUPAL STAGE IN ICHNEUMONIDAE, ILLUSTRATED BY THE LIFE-HISTORY OF *EXENTERUS ABRUPTORIUS*, THB.

By K. R. S. Morris, Ph.D., B.Sc.

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Introduction.

The prepupal stage is a well-known phenomenon, observable in the life-histories of many Lepidoptera and Hymenoptera. Perhaps the clearest and most recent description is that given by Eleiscu (1932) in the case of the pine sawfly, *Diprion pini*, L., in which he shows that there are two distinct phases, the eonymphal and pronymphal, during the resting or prepupal period. The writer has had occasion to study the larval histories of a number of parasitic as well as phytophagous Hymenoptera during the past five years, and has observed that a prepupal phase, comparable in every way with that occurring so typically in the Tenthredinidae, is present in a more or less marked degree in the development of both Ichneumonidae and Chalcididae. (With the Braconidae the author has had no experience.) This has been mentioned in the case of a Chalcid, *Microplectron fuscipennis*, Zett. (Morris and Cameron, 1935), but not yet fully described. In the Ichneumonidae the definite facies of the prepupal stage is more easily observable and more marked than in the Chalcididae. The degree seems to vary also in the different groups of the Ichneumonidae. *Exenterus abruptorius* has been chosen for the present description partly because it exhibits this phenomenon in a more marked degree than in most of the other parasites, also because it has been studied in greater detail than any other. During the past three years several million sawfly cocoons parasitized by this species have been handled in the course of their collection in Europe and export to Canada for liberation against a serious outbreak of a spruce sawfly.

Life-History of Exenterus abruptorius.

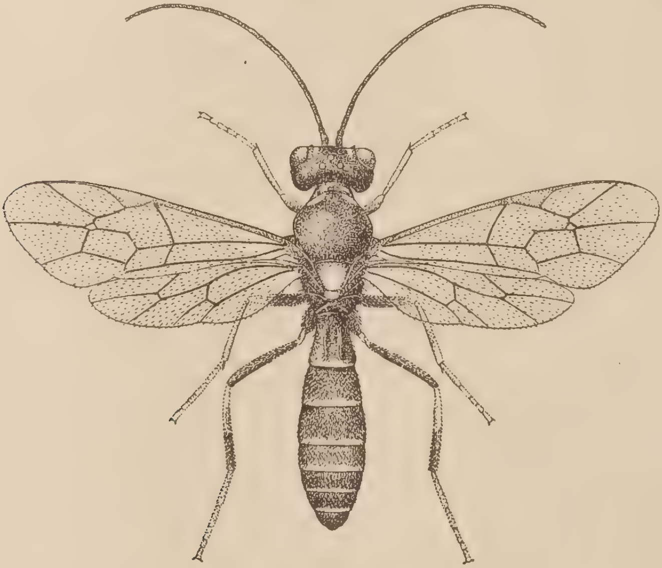
Distribution and Abundance.

Exenterus abruptorius, Thb. (*cingulatorius*, Htg.) is a very important primary parasite of the pine sawfly, *Diprion sertifer*, Geoff. Considering its wide distribution and abundance it is surprising that it has not been observed more frequently by other workers, there being only one previous record from this host, by Schönwiese (1932) and no authentic records from other hosts. Most probably this species has been confused with *E. marginatorius* on many occasions. Schönwiese found it to be the most numerous Ichneumonid parasite on *D. sertifer* in South Carinthia in 1931–32, attaining 55 per cent. parasitism. He gives a short description of its biology, but as this is by no means complete there is no hesitation in giving the present detailed description and illustrations. /l

During the past three years *E. abruptorius* has been found parasitizing *D. sertifer* in Sweden, Poland, Austria and Hungary. It has always been one of the most important species making up the parasite complex, frequently *the* most important, exceeding in abundance even the cocoon parasites, rather an exceptional position for a larval parasite of the Diprionidae. It has never been found in a lower proportion than 15 per cent. of the cocoons, and frequently attained a 50 per cent. parasitism. In Sweden in 1935 and 1936 it was present in 25 per cent. of cocoons in a very large infestation of *D. sertifer*. In Poland in 1936 it was observed in large numbers on the wing in some severe *D. sertifer* infestations, where larvae were still feeding. In Austria in 1934 and 1935 it was present in 15 per cent. of cocoons in some small infestations. In Hungary it has been found in a great many localities, being present in every infestation of *D. sertifer* that has been visited there in the last three years, parasitizing the larvae to an extent ranging from 20 to 50 per cent. In 1936 over twenty million *D. sertifer* cocoons collected near Debrecen in East Hungary showed, in repeated samples, an average of from 45 to 50 per cent. parasitism by this species. This must, then, be considered one of the most successful and important parasites of *D. sertifer* in Europe.

The Adult.

This is a handsome, shining black insect with conspicuous bright yellow markings on body and legs (fig. 1). The head is black above, with the face entirely yellow, except for a black line along the median suture and round the insertion of the clypeus and antennae. The thorax is black with yellow stripes on the neck and shoulders and the scutellum yellow ; closely but finely punctate, so retaining a shining appearance. The black abdominal segments are edged with yellow posteriorly, the bands being all of equal width. Antennae black above on the coxae and femora and hind tibiae. Claws in female pectinate, in male simple. Front margin of mesosternum keeled. This latter character separates this species, together with *E. marginatorius*, from all the other members of this genus. It may be distinguished from *E. marginatorius* by the pectinate claws in the female, by the even yellow banding of the abdomen (in *E. marginatorius* the bands on the first two segments are much broader than those on the following ones), and by the finer punctation of the thorax and abdomen. Average length of males, 8·75 mm., of females 9·25 mm.



Fig, 1. *Exenterus abruptorius*, adult ♀ (× 6).

It is interesting that whereas in Sweden the sexes appeared in approximately equal proportions, in Hungary females were greatly in excess, making up to 80 per cent. and males 20 per cent. of the emergences from naturally parasitized cocoons.

The insect appears to be univoltine, as is the host, adults having been found on the wing in May in Central Europe, but none ever being found after midsummer, neither have they ever emerged during the summer from hosts parasitized early in the year.

The Egg.

The egg (fig. 2 *a*), 0·35 mm. long by 0·28 mm. wide, is broadly oval in shape with the upper surface slightly flattened, with a small knob at one end (the micropyle ?) and at the other the chorion drawn out into a short stalk or pedicel. It is clear, greyish white in colour, with a perfectly smooth, unsculptured surface. It is embedded under the skin of the host larva, the upper surface of the egg projecting slightly through a large oval aperture in the skin, the end of the pedicel projecting through the skin by a separate hole. The whole egg is surrounded by a thick, fairly large layer of fibrosed wound tissue, very dark brown in colour. This makes the egg very conspicuous on the living larva. The eggs are laid on prepupae or fifth stage larvae and may be placed on any part of the body, though usually latero-dorsally in the region of the middle segments. The egg is almost invariably placed with its long axis at right angles to the length of the larva.

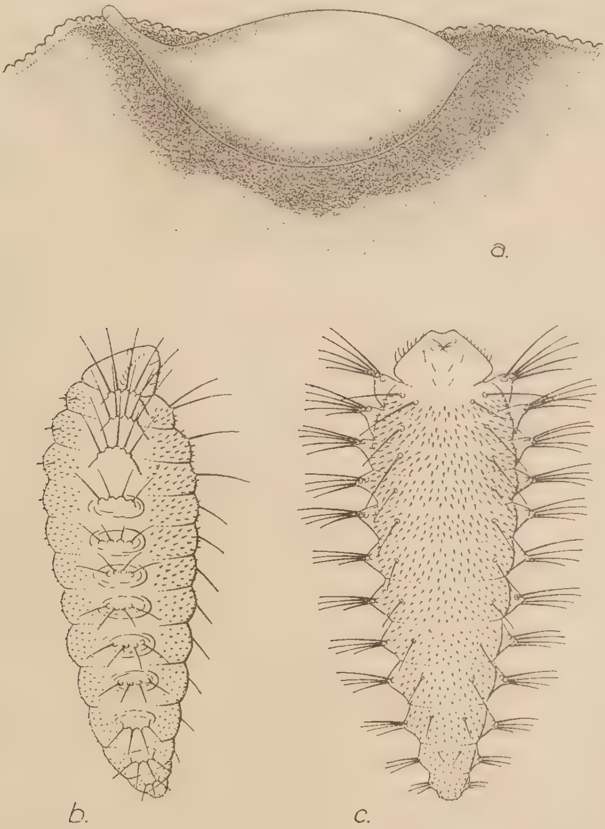


Fig. 2. *Exenterus abruptorius* : *a*, egg (× 100) ; *b* and *c*, primary larva, lateral and ventral views (× 60).

Oviposition has been watched in the field. Females hover around colonies of the gregarious host larvae, seeking apparently for a mature larva isolated somewhat from the others. On finding such a one they approach with the utmost caution, alighting at some little distance from the larva and then stalking it with all the careful and deliberate movements of a predatory mammal. Finally, if the larva has not become alarmed and commenced throwing its head backwards with that typical jerking motion of the sawflies, the *Exenterus* springs upon it and paralyses it almost instantly with a quick thrust of the ovipositor. The egg is then laid under the skin and the parasite departs, the whole process taking place remarkably quickly, in 20 to 30 seconds. Owing to the extreme shyness of the adult parasites this oviposition could not be watched sufficiently minutely for the exact placing of the egg under the skin to be observed. From the position it assumes, however, it is probable that the ovipositor is inserted in the hole subsequently occupied by the pedicel. As the egg flows from the ovipositor it swells and bursts the skin into the oval split through which its surface protrudes. Thus it is held firmly in position by the overlapping of the host cuticle as well as by the pedicel and the knob at each end of the egg. This is of the utmost value for the survival of the eggs, since as has been mentioned, they are sometimes laid on the fifth stage larvae and therefore have to come through one ecdysis, and in any case they will be exposed to the danger of being dislodged by mechanical action when the larva is spinning its cocoon, turning actively round and round within a network of fibrous threads which might easily drag out an egg less firmly fixed. Indeed, in contrasting this species with some others of the genus, notably *E. tricolor* and *E. adspersus* parasitizing *Diprion polytomum* (to be described in a later paper), whose eggs are external to the host skin and attached by a slender stalk, one can understand why these two parasites never attain such a high degree of parasitism or have such a wide distribution as *E. abruptorius*.

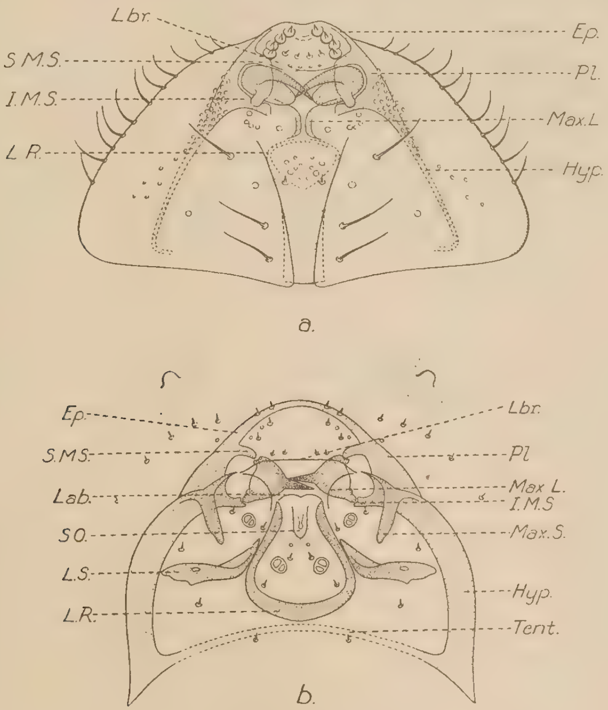
The Larval Stadia.

The primary larva hatches through a split in the upper surface of the egg. Hatching never takes place until after the host prepupa has spun its cocoon, and the period between oviposition and hatching is by no means fixed, showing a considerable, and apparently quite arbitrary, variation with no relation to temperature or climate. For example, in the hot plains of Hungary in mid-May and June, with the mean daily temperature between 18° and 23°C., the variation was from 10 days to over a month in some batches of material. The same irregularity was apparent in the development of the larvae. A small proportion, about 15 per cent., went straight through their development and reached maturity in 3 to 4 weeks. The remainder stayed in the first stadium for varying periods up to two and a half-months after hatching, so that primary larvae could still be found late in August, although oviposition took place at the end of May. This state of affairs was observed not only by watching individual parasites (in which case the artificial conditions of observation might well retard development), but also by repeated sampling of cocoons from the same locality, the development of the parasites being observed on opening the cocoons. The results of one such set of observations is given below as the clearest way of indicating the progress of a generation of *E. abruptorius* larvae.

Table showing State of Development of E. abruptorius *Larvae in* D. sertifer *Cocoons from Izsák, Hungary, in* 1935.

Date	4.vii.	16.vii.	1.viii.	18.viii.	7.ix.
Approximate number of days from spinning of cocoon	36	48	64	81	101
Proportion of primary larvae (per cent.)	85	77	73	29	0
Proportion of older larvae (per cent.)	15	23	27	71	100

Hatching could not have taken place before the spinning of the host cocoons, so that is taken as a convenient zero point. The delay in development always took place in the primary larval stadium ; as soon as the second stadium was entered growth proceeded rapidly, and in 2 to 3 weeks the larvae reached maturity. Thus the separation of primary larvae from older larvae in the table gives a good indication of the proportion of larvae with retarded development and those actively developing or in the normal resting stage as prepupae. It will be seen that in the majority of the larvae (approximately three-quarters) development was retarded for a period of about two months, then, at the end of the summer, the number developing increased rapidly, and by the middle of September all had reached maturity. This description of the development of *E. abruptorius* holds good for the region of Austria and Hungary, where these observations were made. Unfortunately it has been impossible to follow the full course of happenings in Sweden, which would afford a very interesting confirmation or contrast. The significance of such a delay in development is not very clear, unless it be entirely negative ; in such a univoltine parasite and host there is no necessity for a rapid development, such as has been observed in other species of *Exenterus* on the bivoltine sawflies.



Fig, 3. *Exenterus abruptorius* : *a*, head of primary larva (× 250) ; *b*, head of mature larva (× 75). *Ep*, epistoma ; *Hyp*, hypostoma ; *I.M.S*, inferior mandibular strut ; *Lab*, labium ; *Lbr*, labrum ; *L.S*, labial strut; *L.R*, labial ring ; *Max. L*, maxillary lobes ; *Max. S*, maxillary strut ; *Pl*, pleurostoma ; *S.M.S*, superior mandibular strut ; *S.O*, salivary opening ; *Tent*, tentorium.

The primary larva (fig. 2*b*,*c*) measures 0·5 mm. long by 1·17 mm. wide when hatched, but grows to a size of 1·0 mm. by 0·35 mm. before the first ecdysis. It is very hairy in appearance, almost pure white in colour, with a fusiform body, tapering gradually to the tail, but broad in the thoracic region. The strongly chitinized, dorso-ventrally flattened head-capsule (fig. 3 *a*) measures 0·22 mm. across the base. The head bears a pair of small papilla-like antenna antero-dorsally, an almost circular, cup-shaped sucker antero-ventrally, the inner surface of which is armed with 8 strong spicules laterally, 4 weaker ones centrally, and 4 small sensillae basally, the base being bounded by the labrum. Below this is the mouth-opening, with a pair of strong, hooked mandibles bounded basally by the maxillary lobes. Ventrally and basally there is a groove, produced by an inward fold of the chitinous head-capsule. Laterally is an armature of small stiff setae, and three pairs of setae are disposed ventrally. Besides these are numerous sensillae arranged in definite groups, the most conspicuous being two longitudinal clusters overlying the lateral arms of the internal chitinized head-skeleton. The latter is quite simple in the primary larva, consisting of superior and inferior mandibular struts, supporting the mandibles and joined by the pleurostoma. These are produced forward to form the epistoma, bounding the sucker laterally and anteriorly. The pleurostomal rami are produced posteriorly to form the hypostoma, the ends of which join the inwardly projecting tentorium. Below the mouth-opening is a ring-shaped chitinized structure, the labial ring, very much elongated posteriorly. The thirteen-segmented body of the larva has a dermal armature of fine setae, each about 0·015 mm. long on a raised, papilla-like base, closely arranged all over the segments, and of long, strong articulate hairs, up to 0·15 mm. in length, arranged in definite groups. The lateral lobes of the body segments, most developed in the thoracic region, bear groups of 5 hairs in this region, only 4 in the abdominal region. There is also a row of 4 hairs ventrally on the first segment and 2 hairs on each of the other segments, except the last two. The arrangement of these is shown in the illustration.

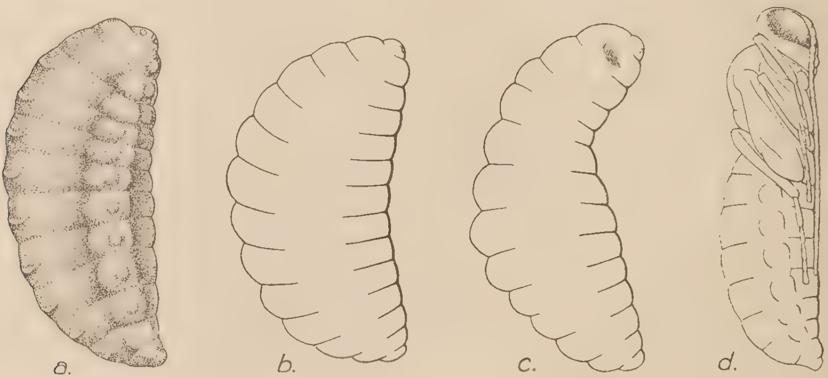


Fig. 4. *Exenterus abruptorius* : *a*, mature larva ; *b*, eonymph ; *c*, pronymph ; *d*, pupa (all × 5).

By means of these hairs and setae the larvae are capable of quick and active movement, and they also derive from them a certain amount of protection from being crushed by the host prepupa, which is not killed until the parasite enters the second stadium. During the whole of the first instar the larva remains fixed to the host by means of its hooked mandibles and sucker. If it is dislodged it will roam about for a short while, but soon regains its hold upon the host. The larva passes through five stadia before reaching maturity. On entering the second stadium the long hairs and the characteristic strongly chitinized head-capsule of the primary larva are lost, and it assumes a form essentially similar to the mature larva, except for the internal head-skeleton, which has not yet reached its full complexity. The fine cuticular setae are retained throughout its life and probably contribute to its powers of active movement. The larva takes on a more active life on reaching the second instar, never remaining fixed for long in one position on the host. If, as occasionally happens, more than one egg has been laid on a host, and more than one larva has hatched, only one larva, that first hatched, ever survives, the others being destroyed during this active roving period.

The mature larva (fig. 4 *a*), measuring 9 mm. in length by 5 mm. in breadth, is strongly curved dorsally and somewhat flattened ventrally and tapers rather more abruptly at the head than at the tail end. There are strongly developed lateral lobes on segments 2 to 12, and conspicuous slightly curved swellings dorsally on segments 3 to 11. Segments 1 to 3 bear small paired papillae ventrally (vestigial legs ?). The cuticle is armed with minute setae, as in the primary larva, slender, 0·02 mm. long, each on a raised papilla-like base. This gives the larva a slightly prickly appearance under low magnification, without concealing the shiny, yellowish-white colour.

The head of the mature larva is considerably smaller in proportion to the body than in the primary larva, and partly sunk in the first segment. It has two conspicuous epicranial lobes dorso-anteriorly, bearing the small papilla-like antennae, each surrounded by a concentrically ringed base. Just above the antennae on each side are two transverse pigmented areas on the epicranial lobes. The strongly chitinized and pigmented mouth-parts (fig. 3 *b*) are very conspicuous, and follow the same plan as in the primary larva. The slender, sharp-pointed mandibles articulate on the superior and inferior mandibular struts. The two superior struts are joined by the narrow epistomal arch, the inferior struts being really a prolongation of the anterior ends of the broad, curved hypostoma. Epistoma and hypostoma are joined by the broad but thinly chitinized pleurostomal rami. To the posterior ends of the hypostoma is attached the inwardly projecting tentorial arch, passing behind the pharynx. From the anterior ends of the hypostomae are forward and inwardly curved projections, the maxillary struts, supporting the maxillary lobes. Below the mouth is the horseshoe-shaped labial ring, supported on each side by the labial struts. The upper ends of the labial ring are joined by the labium, and immediately below this is the U-shaped opening to the salivary duct. The mouth is bounded laterally by the maxillary lobes and anteriorly by the labrum. The latter bears two pairs of small setae along its edges and two pairs of setae and two pairs of sensory pits just below the epistomal arch. Each maxillary lobe bears three setae and a maxillary palp, consisting of two sensory pits surrounded by a chitinous 8-shaped ring. The area within the labial ring also has a pair of similar labial palps, two pairs of setae and two small sensillae. The arrangement of setae on the face outside the areas can be seen in the illustration. Only by the comparative size of these mouth-parts and the minute arrangement of the setae and sensillae can the larvae of the different species in this genus be separated.

The Prepupa.

Four days to a week after the fourth ecdysis the larva reaches maturity, ceases feeding and spins itself a thin, semi-transparent white, papery cocoon inside the host cocoon, the shrivelled empty host skin being excluded. This marks the commencement of the prepupal stage in which the larva rests for the remainder of the summer and until the following spring. This prepupal period is divided into two distinct phases, comparable to the eonymphal and pronymphal stages described by Eleiscu (*l. c.*) and observed by the author in Tenthredinidae.

In the first, or eonymphal, stage there is a slight reduction in length, but the characteristic shape of the fully-fed larva is retained (fig. 4 *b*), strongly curved on the dorsal aspect, almost straight on the ventral, with a perfectly uniform anterior and posterior tapering from the thickest part of the body, which is now in the region of the sixth segment. The lateral lobes become less prominent, and the transverse dorsal swellings and ventral papillae are entirely absorbed. The clear, semi-transparent, yellowish-white colour of the larva becomes an opaque white, largely owing to the accumulated fat-bodies lying in a definite coelomic arrangement just under the skin. The activity of the larva is lost, though the eonymph is capable of a feeble wriggling motion. The mouth-parts are still clearly visible and the mandibles are moved actively when the prepupa is disturbed, though the power of feeding is lost.

The transition to the pronymphal stage is gradual, but the onset may be said to occur when the developing imaginal eyes first become faintly visible. At the same time the body tends to lengthen and becomes almost crescent-shaped, the head and tail being pushed forward and the ventral aspect being curved inwards (fig. 4 *c*). Most characteristic is the marked differentiation of thoracic and abdominal regions by a constriction at the junction of the fourth and fifth larval segments, forming a slight but distinct waist. The abdominal region swells considerably, becoming proportionately larger than in the eonymph, and has the greatest width at the seventh segment. The thorax and head are closely merged and take on a more cylindrical shape, quite distinct from the earlier stage. The lateral lobes have now disappeared. The swelling imaginal eyes develop prominence. The larval mouth-parts are still visible, but the mandibles can no longer move. The pronymph itself has lost all powers of movement. These changes are consequent on the development of the pupa within the old larval skin, which has become detached and loosened and so allows a certain shift to take place inside. Thus the imaginal head now appears to be developing beneath the first segment of the pronymph, the pro-, meso-, and metathorax occupy the second, third, and fourth segments, and the abdomen occupies the fifth to thirteenth segments.

The duration of the eonymphal stage is always much longer than that of the pronymphal, occupying the main part of the hibernation period, that is from summer, throughout the winter, until the end of April or early in May of the following year. Then the transition to the pronymphal stage takes place, and in 5 to 14 days the fifth and last ecdysis is undergone, preceded by defaecation, and the fully-formed *pupa libera* appears.

In the other bivoltine species of *Exenterus* and other ICHNEUMONIDAE that have been studied, the eonymphal stage invariably exceeds the pronymphal in length. In the first or summer generation the eonymphal stage lasts from 4 to 7 days, or three-quarters of the prepupal period, and the pronymphal only 2 to 3 days. In the second or autumn generation hibernation is invariably in the eonymphal stage and the pronymph appears in spring and lasts from a few days to a week before pupation takes place.

The Pupa.

After the last ecdysis the fully formed *pupa libera* appears (fig. 4 *d*). This is at first glistening white, only the eyes being dark red. The antennae, legs and rudimentary wings, are clearly separated. Rapidly the pupa darkens to an almost black colour, and 4 or 5 days after pupation the adult emerges, cutting a ragged, circular hole at one end of the host cocoon.

Hibernation.

It has already been remarked that hibernation in *E. abruptorius* takes place in the eonymphal phase. It is very interesting that in Sweden this species frequently spends two years in diapause in the host cocoon. In the spring of 1935 only 63 per cent. of *E. abruptorius*, overwintering from the summer of 1934, emerged ; the remaining 37 per cent. remained in the prepupal stage and emerged in the spring of 1936. In Hungary the whole of each generation was found to emerge in the following year. It will be remembered that there is another contrast between these two localities, in the sex proportion (see page 526). Whereas in Sweden the sexes are in approximately equal proportions, in Hungary there is a great preponderance of females, which outnumber the males by four to one. The question of parthenogenesis was considered, but its existence could not be proved. An alternative and simpler explanation is that in the more southerly, warmer climates the males are more active and can copulate with a larger number of females than in the north.

These differences in sex proportion (constant during several years' observations) and in hibernation in the two countries again raises the question of the existence of biological races in this parasite. As far as could be ascertained the host has the same habits in both countries.

Conclusions.

In the lower, phytophagous Hymenoptera the prepupal stage is represented by a separate instar, preceded and ended by an ecdysis, and following the five active feeding stages of the larvae. Besides the fifth ecdysis marking the beginning of the prepupal stage there are certain quite distinct colour changes, such as the loss of brightness and conspicuous stripes and markings and the assumption of a general dull hue. Also there is a cessation of feeding, and changes occur in the salivary glands, resulting in the ability to spin a cocoon, there being no powers of spinning during larval life. In this stadium the eonymphal and pronymphal phases are clearly marked. In the first, the prolegs are shrunken and absorbed and the body reduced in length. Rather feeble powers of movement are retained. The pronymph is marked by the first appearance of the future imaginal eyes and by a gradual change in the shape of the body, which becomes distinctly divided into thoracic and abdominal regions. There is now almost complete immobility. This stage is ended by an ecdysis and the assumption of the pupal form. In duration the eonymphal is always longer than the pronymphal stage, in the summer generation being about three times as long, in the autumn generation lasting over the winter until the following spring, when pupation follows four days to a week after the pronymphal phase is entered. When certain TENTHREDINIDAE, notably DIPRIONIDAE, have been found going into diapause one or more years, this has always been in the eonymphal phase.

Now, in the ICHNEUMONIDAE the prepupal stage, divided into eonymphal and pronymphal phases, is shown by a number of species with the typical facies described in the case of *E. abruptorius*. The similarity of these stages with those in the TENTHREDINIDAE is shown by a comparison with the above description. There is the spinning of the cocoon, the cessation of feeding, the reduction in length and of body appendages, and curtailing of movement in the eonymphal stage. In the almost white Ichneumonid grub a marked colour change is not possible, but there is a change in appearance. In the pronymphal stage there is the appearance of the imaginal eyes, the changed shape of the body and the complete immobility. Furthermore, the relative lengths of time occupied by the two phases and the long hibernation and diapause as an eonymph, are exactly the same in the ICHNEUMONIDAE as in the TENTHREDINIDAE. Only one thing is lacking in the comparison, that is the absence of an ecdysis previous to the prepupal stage in Ichneumons. Here there are typically only five instars previous to the pupal stadium, the mature larval stadium merging into the prepupal on the cessation of feeding and the spinning of the cocoon. Apparently, then, in the ICHNEUMONIDAE a whole instar is lost, though the typical facies of the prepupal stadium in the lower Hymenoptera is retained.

Further than this, the degree in which the prepupal facies is exhibited seems to vary in the different groups of the ICHNEUMONIDAE. In those that have come under personal observation the Tryphonines, *Exenterus*, *Lamachus*, *Torocampus* and *Lophyroplectus*, exhibit it in the most marked degree, whereas in the Cryptines, *Microcryptus* and *Hemiteles*, it is less apparent. It is suggested here that a more complete and comprehensive study of this phenomenon might throw interesting light on the relationships and phylogeny of the ICHNEUMONIDAE, and if pursued further, of the higher Hymenoptera.

Summary.

A full description is given of the life-history of *Exenterus abruptorius*, Thb., an important parasite of the pine sawfly, *Diprion sertifer*, Geoff.

The insect is univoltine, like the host. It oviposits on the last stage larva or prepupa and only hatches after the host has spun its cocoon. Only one-quarter of the primary larvae develop immediately, the remainder resting up to two and a-half months during the summer before proceeding with their development. On the completion of feeding the parasite larva spins its cocoon within the host cocoon and enters the prepupal stage, which can be divided into two distinct phases, eonymphal and pronymphal. Hibernation is always in the eonymphal stage. In Sweden 37 per cent. of this species remained in hibernation for two winters, but in Hungary all emerged in the spring following the year of development. Further than this, in Sweden the sexes were in approximately equal proportions ; in Hungary females exceeded males by four to one. This may indicate the existence of biological races.

Other ICHNEUMONIDAE exhibit the prepupal stage, with eonymphal and pronymphal phases, in their development. The typical facies of this is analogous to that in the prepupal stage in TENTHREDINIDAE, in which, however, ecdysis precedes this stage, which is then a distinct instar. It is suggested that an instar is lost in the development of the ICHNEUMONIDAE, though the facies of the prepupal stage is retained.

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A NEW GENUS OF MALAYAN CAPSIDAE (RHYNCHOTA) FROM ARECA PALM.

By N. C. E. Miller, F.R.E.S., F.Z.S.

The Capsid described in the present paper came under observation in Malaya some years ago but was not then specifically determined. Mr. W. E. China, of the British Museum (Natural History), was kind enough recently to examine it, and came to the conclusion that a new genus should be erected to contain it. Specimens were returned to me by Sir Guy Marshall, Director of the Imperial Institute of Entomology, along with some notes made by Mr. China which would be of use in the preparation of the diagnosis of the new genus.

I am greatly indebted to Mr. China for his assistance and to Sir Guy Marshall for affording me the opportunity of describing the genus.

Types and paratypes have been deposited in the British Museum and paratypes in the Selangor Museum, Kuala Lumpur, F.M.S. Additional paratypes are to be found in the collections of the Entomological Division, Department of Agriculture, S.S. and F.M.S.

Family CAPSIDAE.

Subfamily Heterotominae.

Parasthenaridea, gen. nov.

Antennae about as long as body ; segment 1 as long as anteocular portion of head, cylindrical, thicker apically than basally ; segment 2 four times as long as 1, feebly thickened towards apex ; segments 3 and 4 slender, 3 half as long as 2, 4 two-thirds as long as 2. *Eyes* large. *Head* (including eyes) about twice as broad as long, moderately deflexed ; from the side shorter than height at base ; vertex between the eyes somewhat flattened and with the basal margin carinate ; clypeus moderately rounded ; rostrum reaching apex of posterior coxae. *Pronotum* somewhat flattened, about twice as broad as long at its widest part, its sides broadly rounded and basal margin feebly sinuate. *Scutellum* triangular, its base feebly raised and not entirely covered by pronotum. *Hemielytra* with the membrane extending beyond the apex of abdomen, smaller membrane cell triangular. *Wings* with a hamus in basal cell. *Legs* : hind femora moderately incrassate ; tarsi with a bilobate arolium, the apices of which are truncate and widely divergent.

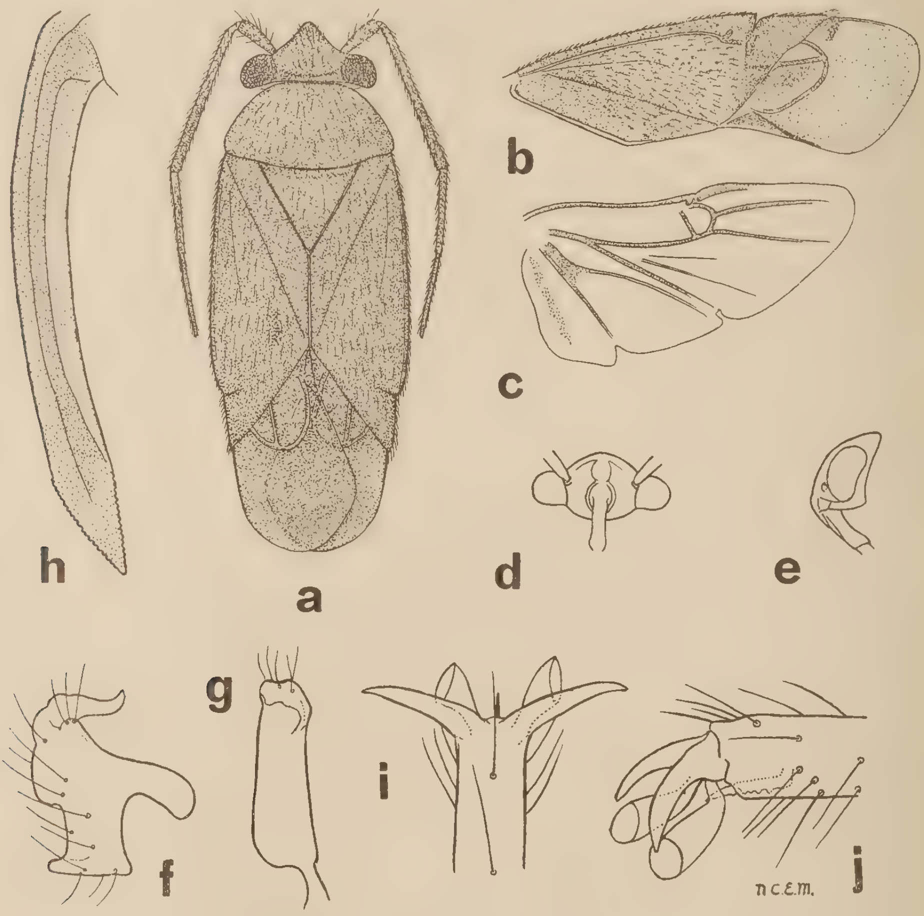
Mr. China who examined this new genus kindly sent the writer the following observations.

This new genus belongs to the subfamily Heterotominae in which the arolia are large, membranous and usually convergent at apices. It is allied to *Sthenaridea*, Reut. (Ent. Tidskr. **5**, p. 197, 1884) but differs in the much shorter antennae and in the presence of a hamus in the hind wing cell. Furthermore, there is a close resemblance with *Sthenarus* (Phylinae, in which the arolia are bristle-like), but it differs in the presence of large divergent arolia.

Parasthenaridea arecae sp. n. (fig. 1).

Colour : segment 1 of antennae dark ferruginous ; segment 2 dark ochreous with the apical third ferruginous ; segments 3 and 4 testaceous. Eyes dark purplish brown. Head, body, corium and legs olivaceous ; corium subhyaline, legs pale olivaceous ; membrane hyaline, very faintly infumate in the basal costal angle and faintly iridescent. Wings hyaline, iridescent, venation testaceous.

Body ovate, shining ; *eyes* from the side sub-reniform ; facets convex. *Antennae* : segment 1 with a few moderately robust and moderately long sub-erect setae and short recumbent setae ; remaining segments with short, forwardly directed sub-recumbent setae. *Head*, *pronotum*, *corium* and *abdomen* ventrally moderately densely setose, the setae on corium arising from punctures. *Tibiae* armed with numerous forwardly directed spines.



Fig, 1. *Parasthenaridea arecae*, sp. n. : **a,** adult ; **b,** elytron ; **c,** wing ; **d,** head from front ; **e,** head from side ; **f,** left paramere ; **g,** right paramere ; **h,** ovipositor ; **i,** apex of tarsus from above ; **j,** apex of tarsus from side.

Length, head and body, ♂ 2·20 mm., ♀ 3·20 mm., hemielytra, ♂ 2·30 mm., ♀ 2·60 mm.; width across base of pronotum, ♂ 1·00 mm., ♀ 1·20 mm.

Described from a long series taken mostly by Mr. H. T. Pagden of the Department of Agriculture, S.S. and F.M.S.

Notes on Developmental Stages.

P. arecae is an abundant insect and has been found, up to the present, exclusively on the inflorescence of the Areca palm (*Areca catechu*, L.). In view of the fact that before it begins to produce flowers the Areca palm has attained a height which renders observation of insects associated with its inflorescence a difficult procedure, investigations in the field have not yet been carried out. Hence it is not definitely known whether *P. arecae* is of economic importance or not. Nevertheless, after having kept a number of both larvae and adults under laboratory conditions for some time, the impression was gained that they feed exclusively on the flower stalks. Whether serious damage is caused, which would result in the premature fall of flowers, is uncertain.

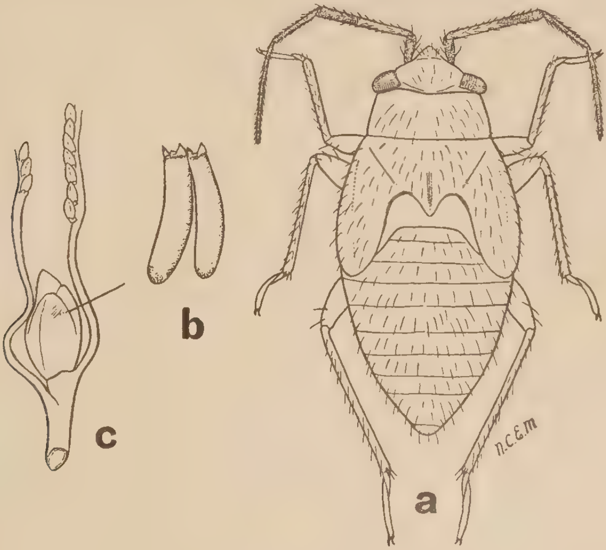


Fig. 2. *Parasthenaridea arecae*, sp. n. : **a**, fourth instar larva ; **b**, ova ; **c**, part of inflorescence of *Areca catechu*, L., showing site chosen for oviposition.

The ova, which are approximately 1 mm. in length, are deposited under a female flower calyx and in that situation are invisible (fig. 2). After the emergence of the larva, however, the greater part of the empty and flattened chorion may be seen protruding from under the calyx. In shape, the ova are cylindrical, feebly curved, and compressed at the opercular end. The margin of the opercular rim is narrow, but enlarged at opposite sides to form a triangular projection. The colour is pale ochreous, with the opercular end narrowly suffused with ferruginous and the opercular rim white. They are deposited either singly or in batches, the greatest number observed in a single batch being nine.

As regards the larvae, they are closely similar both in colour and in shape throughout the course of development with the exception that rudiments of the hemielytra begin to appear in the 3rd instar. The colour of the 4th instar larva (fig. 2) is as follows :—Eyes dark ferruginous ; head, thorax and rudimentary hemielytra dark olivaceous. Abdomen green. Segment 1 of antennae dark ferruginous ; segment 2 ochreous with a narrow suffusion basally and a broad suffusion apically ferruginous ; apical segments testaceous. Setae on antennae pale ferruginous, on thorax and rudimentary hemielytra fulvous, on abdomen dark ferruginous. In the previous instars the colour of the head and body is green rather than olivaceous.

THE SENSES OF SMELL AND SIGHT IN *GLOSSINA SWYNNERTONI.*

By S. Napier Bax,
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W

(Plates XIII and XIV.)

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1. Introduction.

The relative importance of the particular senses employed by tsetses to find their hosts has been the subject of much observation, work and debate, and the fact that the problem has not been resolved long ago is due to the difficulty of devising satisfactory experiments. It is agreed, however, that the choice is limited to the senses of smell and sight. On the one hand, there is the school of thought represented by Nash (1930, p. 254) experimenting with *G. morsitans* and Harris (1930, p. 35) with *G. pallidipes*, which concludes that the tsetse hunts its food by sight ; while on the other hand that of Claude Fuller and Mossop (1929), working with *G. pallidipes*, tends to disparage the sense of sight and believes that the tsetse has a keen olfactory sense and can be led to its quarry by the sense of smell. Between these extremes lie the majority of workers whose views as a result of observation and experiment agree with those of Swynnerton (1936, p. 205), who, after a full review of the work done up to that time, considers that both scent and sight are important. In conclusion, it must not be forgotten that the relative importance of these two senses may vary with the species of tsetse.

The purpose of these experiments was to isolate and test the powers of smell and sight of *G. swynnertoni*. They have been carried out without mutilation of the insect, as this is liable to give rise to more questions than it solves. A satisfactory technique was evolved only after considerable thought and trial, and in the light of experience this could be much improved. The writer hopes that the method employed may be of use to other workers faced with similar problems. The unwieldiness of the " apparatus " may appal English entomologists, but those working in the tropics know how cheaply grass fences can be erected with native labour.

The powers of smell were assessed by measuring the reaction of tsetses to a team of hidden oxen passing across the wind at ever increasing ranges. Oxen were chosen because they are known to be attractive to *G. swynnertoni*. In addition, the scents from certain other objects were tried. Sight was tested by employing the same team of oxen as a target. A few experiments were also done on tonal contrast and with a smaller target.

Finally, it must be mentioned that the experiments had to be fitted in with other and more pressing work and in the time available the writer could not develop the theme as he wished. Nevertheless it is believed that definite light has been thrown on the comparative value of smell and sight to *G. swynnertoni*, and the actual distances at which it can smell and see under certain conditions.

2. Acknowledgments.

The scent experiments—particularly those with a calf-trap—undertaken by Mr. Swynnerton, Director of the Department of Tsetse Research, have encouraged the writer to carry the investigation a stage further. He desires to pay tribute to the inspiration he has received from this previous work. He is indebted to Mr. Potts, of this Department, for fruitful discussion at the time of the experiments and for useful suggestions after reading the manuscript. He wishes to thank Dr. Gunn, of Birmingham University, for preliminary advice regarding the statistical treatment of the figures. Dr. Jackson, of this Department, is responsible for the statistical examination of the results and the writer records his great appreciation of this help. Thanks are also due to the writer's sister, Mrs. Hicks, who drew the figures. Finally, he is glad of the opportunity of thanking Mr. Rosch, of the Department, for the pains he took in constructing the cages for the experiments—not only those illustrated, but other types that were tried and discarded, and for taking the photographs.

3. The Site of the Experiments.

The experiments described in this paper were carried out at the Headquarters of the Tsetse Research Department at Old Shinyanga in the Lake Province of Tanganyika Territory. Here the local aerodrome afforded a convenient and large open space, not quite level but sloping gently from the north-west to the south-east. It was very well suited for the scent experiments, as its length lay with the wind, but was not quite so satisfactory for the sight experiments, as the conformation of the ground imposed restrictions.

Old Shinyanga has an altitude of just under 4,000 ft. The experiments were done over a period from the latter end of April to the beginning of August, that is, during the long dry season. At that time of the year the early mornings are cool but the days are hot. The sky is generally cloudless and a strong easterly or south-easterly wind blows up till midday. The mean screen temperature at 10 a.m. for the days of experiment was approximately 72°F. The Shinyanga climate has been described by Lloyd (1935) and his paper should be referred to for further details.

4. Scent Range Experiments with Oxen and Men.

(*a*) *General Description.*

In these experiments a cage containing the tsetses was placed in the centre of a circular grass enclosure. After a control period of observing the tsetses a span of oxen was driven to windward of the cage in such a manner that the wind blew from the oxen to the tsetses, while the intervening fence ensured that they were invisible to each other. Then followed a further control period. An observer sat to leeward of the cage and recorded the movements of the tsetses in it.

(*b*) *The Enclosure* (Plate XIII, fig. 1).

The experiments might have been carried out with only a short length of grass fence between the oxen and the tsetses, but it was considered desirable that the latter should be exposed to as little extraneous disturbing movement as possible, and accordingly a complete circle was erected round the cage. It was hoped to make the fence of such a height that not only all movement on the ground would be shut off, but also that the far tree-line too would be invisible to the tsetses, whose view would then be restricted (except for the observer and the flag mentioned later) to the patch of short grass inside the enclosure, the smooth and even sides of the fence and the sky. That ideal was not quite obtainable, for while the fence for practical reasons could not exceed a certain height, the circumference of the circle had to be sufficiently great to ensure the scent-bearing wind finding its way past the obstacle to the cage. Thus, although the bush-line as a whole was quite invisible, yet at two or three points the tops of distant but particularly tall trees could be seen. The circular grass enclosure was constructed then, 60 ft. in radius and 6 ft. 6 ins. high, measured vertically. The fence was built in such a manner that it leaned outwards—basin-like—at an approximate angle of 70 degrees in order to diminish the intensity of the shadows thrown when the sun was not yet vertical. This was to provide as far as possible an equal light-value in all directions during the mornings when the experiments were carried out. The bottom of the fence did not quite reach to the ground, a gap of 9 ins. (vertical) being left below in order to facilitate the entry of the scent-bearing wind. Tests were made to ensure that the tsetses could not see the feet of the oxen through this gap or the heads of the driver and *voorlooper* (leader) over the top of the fence. The greatest care, too, was taken that there were no chinks in the fence itself and that none developed.

(*c*) *The Ox Arcs* (fig. 1).

Experiment proved that even on days when apparently the wind was blowing constantly from one single direction, in actual fact it was frequently veering slightly. Thus something more was required than the simple procedure of driving into the ground a peg at a certain range directly up-wind of the cage and recording the reaction of the tsetses as the oxen walked past the mark, for they might arrive at an unlucky moment when the wind was " off." The greater the range the greater the possibility of error. To overcome this difficulty the device was adopted of making the oxen follow an arc, described at the desired radius, *i.e.*, range, from the centre of the grass enclosure. The length of the arc described by the oxen was dictated by the vagaries of the wind, but its extremities were so arranged that the scent of any object stationed there could not possibly be carried inside the enclosure even when the wind veered into the most favourable quarter for it. Arcs were accordingly laid out at the different ranges to be tested and the grass between them and the enclosure kept short. At the 300 ft. arc (measured from the centre of the enclosure) a flagstaff was erected of such a height that the flag was just visible to the observer when he was seated behind the cage. The flapping flag was within the line of vision of the tsetses, but there was no evidence at all that they were disturbed by it. By keeping an eye on the flag the observer was kept informed of the direction of the wind and would be immediately warned should any serious alteration take place.

(*d*) *The Scent Cage* (Plate XIII, fig. 2).

In the few experiments undertaken before the 26th June the cage containing the tsetses was made of white mosquito netting with a mesh of 10½ to the inch. After that date a straw-coloured curtain net was used of a square mesh 7½ to the inch. It was hoped that the wind would pass through this latter material more easily, but experiments with an anemometer seemed to show that there was little difference. Possibly the coarser threads of the curtain net were a handicap. In both cases the cage measured 77 ins. long by 22 ins. wide by 26 ins. high and stood with its base 26 ins. from the ground. It was attached by lacing to keep it rigid and borne within a wooden framework larger than itself so as not to shelter it from the wind. This was placed in the centre of the enclosure with its long axis lying with the wind, so as to afford the tsetses the maximum opportunity of demonstrating their reaction to any scent received. An anemcmeter stood outside the cage on a projection from the frame. The extent to which the velocity of the wind was affected by the enclosure and cage is discussed later.

(*e*) *The Tsetses.*

The tsetses used in these morning experiments were collected the previous evening. This method ensured hunger and enabled advantage to be taken of the strong and constant wind that so often failed in the afternoon. The sexes were immediatley separated. On inspection in the mornings there was generally seen to have been considerable mortality, but the greatest care was taken to select only thin but lively and apparently normal flies for the experiments.

It would have been more satisfactory to have "hunger-staged" the tsetses, according to the method evolved by Jackson (1933), but that system of diagnosis does not apply to captive tsetses.

The sexes were never mixed in the scent cage and male *G. swynnertoni* were used in all the experiments except when it was desired to discover whether the female reacted similarly. Generally no more than ten tsetses were placed in the cage at one time as it was found difficult to record the movements of a greater number.

The tsetses survived in the cage remarkably well, and it was only occasionally that one had to be replaced during a morning's work.

(*f*) *The Oxen.*

A span of six black oxen of the common small, humped Zebu type was employed. A native *voorlooper* (youth to guide them) was at the span's head and a driver in charge.

(*g*) *The Observer* (Plate XIII, fig. 2).

The writer observed all the experiments personally. He sat on a low stool, with notebook and small clock in hand, 3 to 4 ft. to the leeward end of the cage. That is, he was in full view of the tsetses but out of their line of scent ; nevertheless he must have formed a certain visual counter-attraction, and that fact should be borne in mind when studying the results of the experiments. Positions farther away from the cage were tried, but elsewhere it was found difficult to observe the movements of the tsetses with certainty. Care was taken to make no abrupt movements, but notes were written freely, and occasionally the writer had to twist his body to get a clearer view of the roof and corners at the far end. No movements of the tsetses could definitely be attributed to these gentle but considerable actions.

No claim is made that every single movement was observed and recorded. It is possible and indeed probable that some were missed. During the many preliminary trial experiments the writer found, however, that his powers of observation rapidly improved, and he is satisfied that any omissions that occurred could not affect appreciably the results that are shown in this paper.

(*h*) *The Routine of an Experiment* (fig. 1).

Each experiment was divided into three periods : (i) the Preliminary Control Period, during which no scent could reach the cage ; (ii) the Passage of Oxen Period, during which the oxen traversed the arc and scent might be received ; and (iii) the Final Control Period, during which again no scent could reach the cage. Before the start of an experiment the observer, whose seat was at A (fig. 1), walked round the cage B and tapped the sides to stir the tsetses and make certain they were active and then waited a short period to give them time to settle down again. The experiment then commenced with the Preliminary Control Period of five minutes. In the meantime the span of oxen was stationed at C, fifteen to twenty paces from the end of the arc DE, awaiting the order to traverse it. Just before the five minute period was up the observer called to a native stationed at F, twenty yards or so away from the enclosure on the leeward side, to signal to the oxen to start. The observer became very skilful at timing the start so that the front ox passed the point D just as the first five minute period closed. As it did so, the driver shouted to that effect for the information of the observer, and the Passage of Oxen Period had begun. The span then moved across wind along the arc DE, and as the hindmost ox passed E the driver shouted again and the period closed. With practice the pace of the oxen became so constant that even on the long arcs their time for the distance varied by only a few seconds. If a particularly quick or slow passage were made—to increase or decrease the allotted time of the Passage of Oxen

Period when taken to the nearest quarter minute—the experiment was generally started again. Then followed a further control period of five minutes, the Final Control Period, with the oxen standing at G.

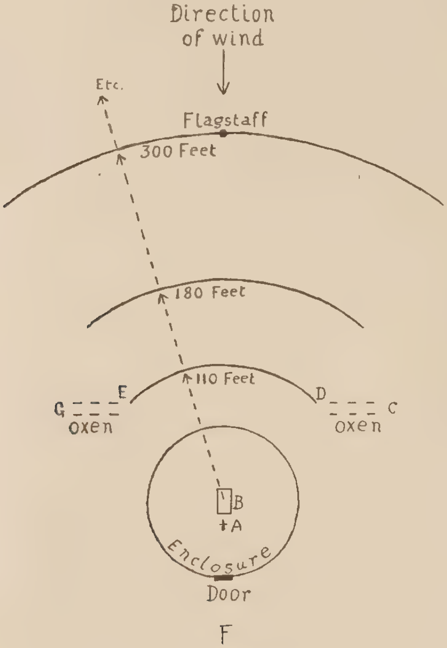


Fig. 1. Plan of scent enclosure and ox arcs.

Before the start of the succeeding experiment the cage was turned, and now the span of oxen moved in the opposite direction from E to D.

(*i*) *Definition of what constituted a " Movement " of a Tsetse in the Scent Experiments.*

It has been mentioned that the shape of the cage was oblong in order that tsetses sitting at the end furthest away from the oxen might be given the chance of flying the whole length towards them when their scent arrived. Such a movement after all would be the most convincing. But it was of course not practicable to devise a means of enticing all the tsetses to the correct end in readiness for such a demonstration. At the moment of arrival of scent at the cage they were situated as they had distributed themselves during the Preliminary Control Period—some at the observer's end, some in the middle, and the remainder already at the end nearest the oxen. To have restricted the meaning of " movement " to actual flight would have meant that the tsetses at the oxen end of the cage, although they might have reacted simultaneously and significantly by breaking into a dance, would have been " disenfranchised." The term " movement " therefore was quite literally interpreted and refers to movement of position of any kind, whether a walk of a fraction of an inch only, a hop from one point to another, a dance or a flight. Each movement of whatever kind has accordingly been given the value of 1 in the diagrams. There still remained, however, the problem of the individual restless tsetse which might dance and rest alternately many times, neither each dance nor each rest lasting longer than several seconds. Such might be regarded as many movements or as a single one. It was finally thought best to fix an arbitrary limit and to count the process as a single movement until an interval exceeded fifteen seconds in length. Scoring was governed by the following rules then :—

1. Every movement of position (subject to the modification in 2) of every tsetse counted as a " movement."
2. When a fly danced and rested alternately the process was regarded as a single movement until an interval exceeded fifteen seconds.
3. If the movement of a tsetse commenced in one period and ended in another, the period in which the movement was initiated scored the point.

While diagrams based on the above scoring methods indicated well enough increased activity in any period, they did not explain the kind of movements that took place and thus often failed to bring out their full significance ; for instance, a flight was not differentiated in the diagrams from a walk. Appendix A therefore has been added to supply this information and reference should be made to it in any close study of the experiments.

(*j*) *The Diagrams.*

This paragraph will be clearly understood if the reader follows the description with one of the scent diagrams before him. Each experiment is represented by a diagram divided into three main sections corresponding to the Preliminary Control, Passage of Oxen and Final Control Periods. The first and last of these sections have been divided into one minute periods, further subdivided into quarter-minutes. The numeral shown on any line in these two sections (Preliminary Control and Final Control Periods) represents the total movements of tsetses initiated within a period measured from 7½ seconds before the time indicated by that line to 7½ seconds after it, that is, the number of movements per quarter-minute. The Passage of Oxen Period has not been divided into minutes or quarter-minutes (but is of course drawn to the same scale as the other periods), for the greatly increased number of movements in this period, especially at the shorter ranges, made it impossible to keep a record of the time of each. In this case the " floating " line on which the numeral is written indicates as before the initiation of movement by that number of tsetses within a period of fifteen seconds. The line does not indicate the exact time the movement was initiated in the Passage of Oxen Period (and for this reason is not shown as stretching right across the column) but must only be interpreted as an indication that *at some time* within that period so many tsetses moved within fifteen seconds. The " floating " lines have been placed arbitrarily in the middle of the Passage of Oxen Periods. Other movements within the Passage of Oxen Periods are of course shown in their general relation to the main movement. Sometimes these amounted to a second mass movement, at other times they were only individual.

It will be seen that in early experiments the Passage of Oxen Periods varied even on the same day. At that time the driver and oxen were not trained to move at the even pace that they afterwards attained. At the greater ranges the ox arcs were longer as veering of the wind became a more important factor ; this accounts for the longer Passage of Oxen Periods at those ranges. Sometimes dancing persisted right into the first minute of the Final Control Period. Therefore in the later experiments a Lag Period was introduced (immediately following the Passage of Oxen Period) to give the tsetses time to settle down. Movements initiated in that period are not shown.

(*k*) *Oxen and Men at* 110 *ft.* (fig. 2).

Fig. 2 shows the results of six experiments with male *G. swynnertoni* and two men. The ragged appearance of the first group of experiments is due to the fact that these were among the earliest carried out, when synchronisation was bad and the natives and oxen not yet adept. The second group belongs to a later phase when a Lag Period had been introduced and the participants had had more practice.

It will be noticed too that on the day the first group was done the anemometer recorded a wind of only 1½ m.p.h., which was also gusty and veering. On the day of the second and third groups it was much steadier (which meant of course shorter ox-arcs) and much stronger—5 and 5½ m.p.h.

It will be seen that a very large number of movements took place in the Passage of Oxen Periods of all the experiments at this range except No. 3. Reference to notes made at the time shows that in that case a lull came as the oxen were passing, and doubtless that accounts for the comparatively poor reaction. The two groups of movements shown in Experiment 2 may have been due to the wind veering during the Passage of Oxen Period and the cage receiving the scent on both occasions, but the observer detected it only on the second. A total of eleven tsetses are shown as having reacted, which means that one moved twice as there were only ten in the cage. Such " plural voting " was of course equally open to the tsetses in the control periods, always provided that a period of fifteen seconds elapsed between the end of one movement and the commencement of another.

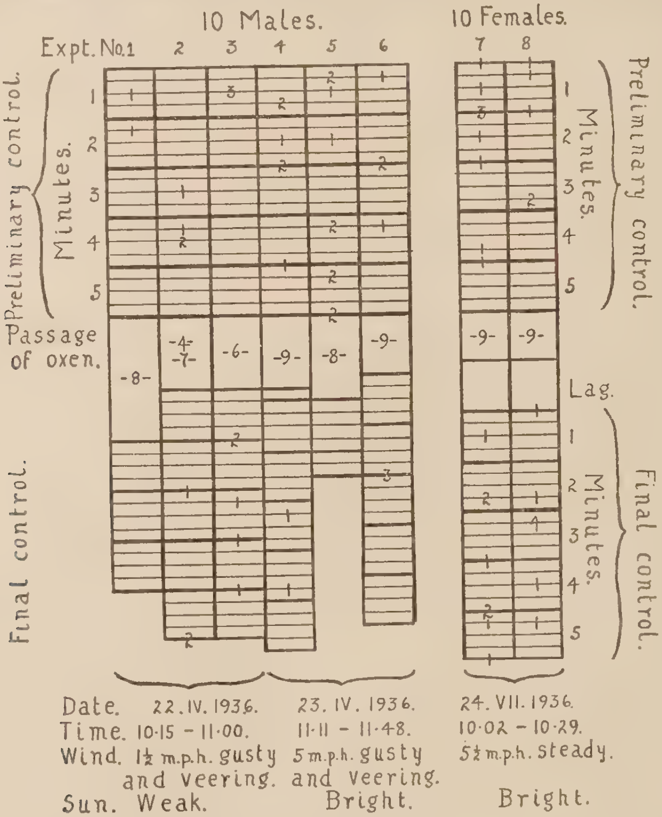


Fig. 2. Scent : 6 oxen and 2 men at 110 ft.

It will not be out of place to describe here the sequence of events in the Passage of Oxen Period of Experiment 1, for that is typical of the other Passage of Oxen Periods at 110 ft. and brings out certain facts which are of great significance.

The observer called to the native stationed behind the enclosure to shout to the driver to start, and presently the driver in his turn shouted to the effect that he was entering the ox arc. None of these three shouts had the least apparent effect on the tsetses in the cage. Once the oxen moved off the shuffling of their hoofs through the grass and the jingling of the trek-chains became louder and louder. As the span arrived at a point exactly up-wind the sounds were at their maximum. Gradually they began to recede and then suddenly the observer seated behind the cage received the sweet smell of the oxen. Up to that time not a single movement had taken place in the Passage of Oxen Period, but now instantaneously with the reception of the scent by the observer, four tsetses from his end of the cage and two from the middle flew to the end next to the oxen and with two more tsetses already there—that is eight out of the ten—danced violently. The synchronisation of arrival of scent as perceived by the observer and the movement of tsetses was most impressive. Slowly the dancing lessened until at the close of the period, signified by a shout from the driver, the tsetses were once more quiescent.

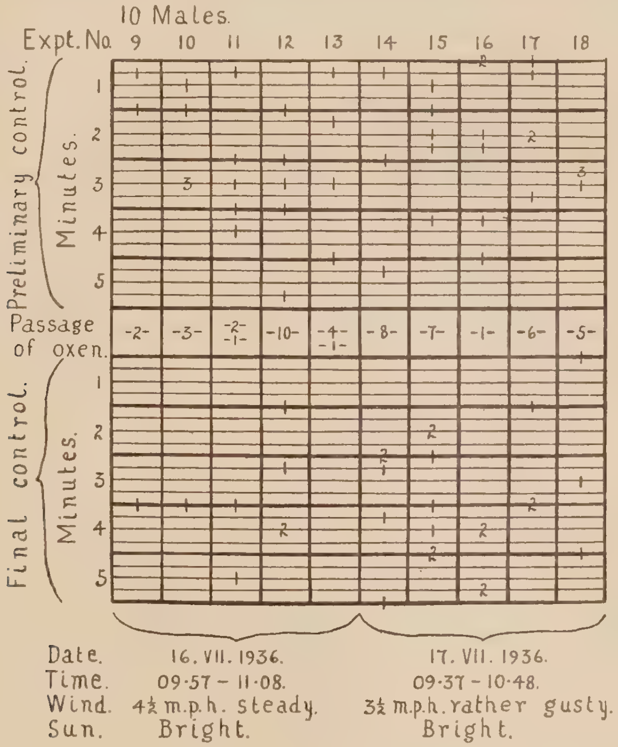


Fig. 3. Scent : 6 oxen and 2 men at 180 ft.

The first significant fact is that sound—or at any rate the kind of sound to which they were exposed in this experiment—had no effect on the tsetses, and the same was observed through the whole series of scent experiments, though naturally certain sounds became fainter at the greater ranges. It should be particularly noted that the tsetses did not react (especially at the longer ranges) until after the sound of the oxen moving had reached its maximum and was becoming fainter. The second significant fact is that in all the experiments at this range, except no. 3, when the wind failed, the observer himself received the scent of the oxen and simultaneously with his detection of it the tsetses reacted. That was a most spectacular and striking confirmation that the scent alone was responsible for the movement of the tsetses.

(*l*) *Oxen and Men at* 180 *ft.* (fig. 3).

Ten experiments were carried out at this range spread over two days. At this distance the scent of the oxen was never detected by the observer.

It will be seen that while the results are less regular and not so spectacular as at the closer range of 110 ft., they are still impressive. In Experiment 16 the wind was noted as very light.

(*m*) *Oxen and Men at* 300 *ft.* (fig. 4).

Ten experiments spread over two days were undertaken at this range. In the second group it will be seen that a Lag Period was included. It will be noticed that the Passage of Oxen Period lasted one and a-half minutes as against one minute in the previous experiments. The greater range made a longer ox arc necessary, which resulted in a longer Passage of Oxen Period.

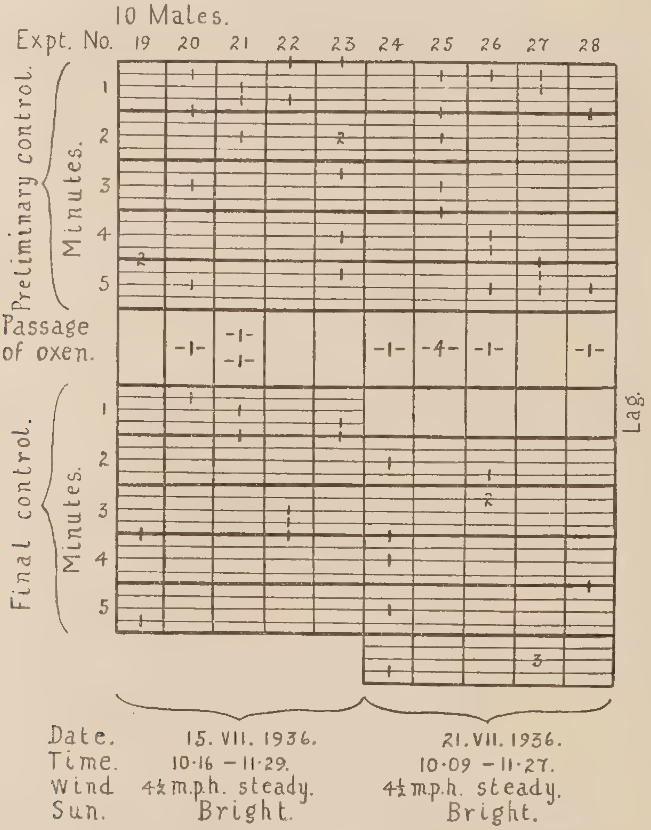


Fig. 4. Scent : 6 oxen and 2 men at 300 ft.

No detailed description of these experiments is given in the Appendix, for it is obvious at a glance that little, if any, reaction was taking place. It is just worth noting, however, that in the Passage of Oxen Period of Experiment 25, in which four tsetses moved, three of these simultaneously flew from the observer's end to the end next to the oxen and danced together with one tsetse already there. It is possible that scent may have been received on that occasion.

5. Scent Experiments with Men.

In order to test whether the tsetses would react to the scent of man, experiments were staged on exactly similar lines to those with the oxen, but with natives in place of the oxen. Reference to fig. 5 shows that in some of the experiments two men were used, in others eight. When two were employed they were intended to correspond to the driver and *voorlooper* walking with the span in the scent experiments with oxen—and were in fact the same natives—and, therefore, to indicate whether human scent was playing a part. On the other hand the group of eight men corresponded to the eight entities in an oxen experiment, six labourers chosen haphazard from the station hands taking the place of the oxen, and the driver and *voorlooper* appearing again.

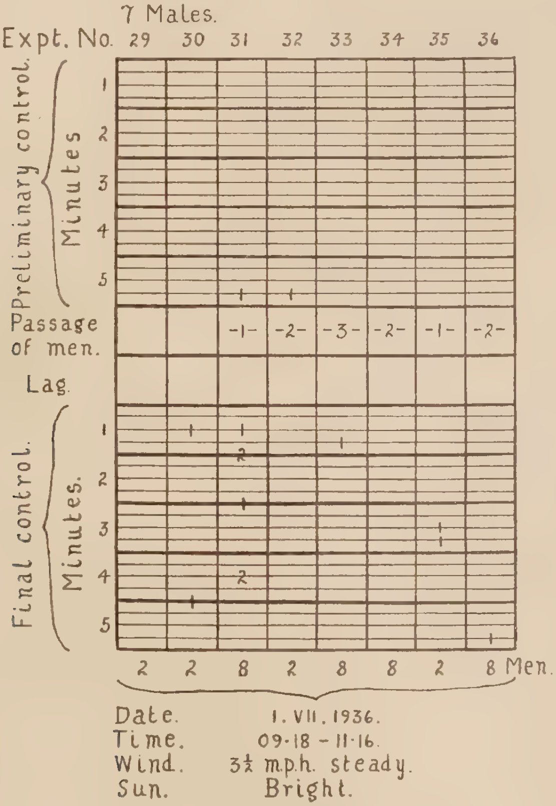


Fig. 5. Scent: Men at 110 ft.

In all these experiments the men walked past in single file and in no case could their scent be detected by the observer at the range at which they were carried out (110 ft).

It will be seen that while there was little appreciable reaction with two men there was more with eight. Taking the diagram as a whole there is statistical evidence that the tsetses were reacting to the scent of the men, but the results seem to show that human scent was playing a negligible part in the oxen experiments.

6. Other Scent Experiments.

(*a*) *Kamba at* 110 *ft.* (fig. 6).

This is the name the natives have for the cambial layer they strip from numerous species of trees and use for tying and binding purposes, particularly in the construction of houses. It was chosen for its very strong onion-like odour which, if attractive, might have been utilised in tsetse traps. The custom is to soak it in water before use, which incidentally increases its smell. Soaked *kamba* was used in these experiments.

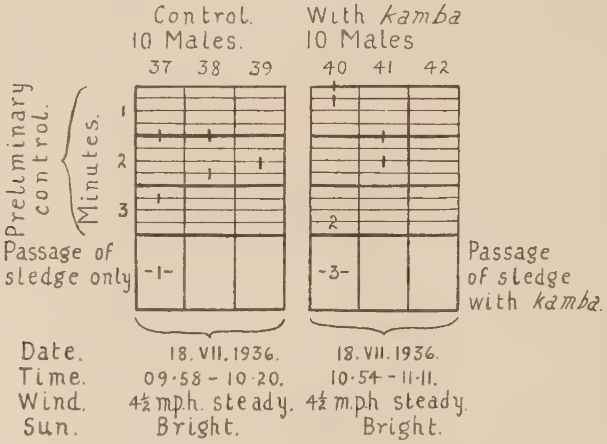


Fig. 6. Scent : *Khamba* at 110 ft.

A sledge was made by nailing a rectangular tray of sheet iron on to an inverted cradle (the wooden form used in building arches (Plate XIII, fig. 3)). The *kamba* was piled on to the tray and a wire attached to the sledge of such a length that men hauling on it could stand in a position where the tsetses could not receive their scent, *i.e.*, at the ends of the arc. While this technique ensured that the tsetses did not receive the scent of the men, yet it had this weakness : the sledge could only be drawn in a straight line across the front of the enclosure and did not follow the curve of the arc as in the other experiments. Thus only if the wind were blowing exactly true would the range be 110 ft. The scent of the *kamba* was so powerful that it could always be detected easily by the observer as it passed on the sledge.

Through press of other work it was not possible to make these experiments as elaborate as the previous ones, and consequently the Final Control Period was omitted and the Preliminary Control Period cut down to three minutes. Nevertheless had the scent of the *kamba* been very attractive it is considered that that fact would have emerged.

Referring to fig. 6, it will be seen that three controls were first carried out, the sledge being drawn past the enclosure empty, except for a length of old sacking which was to protect it from contamination. Three big rolls of *kamba* were then loaded and the second group of experiments carried out. In Experiment 40 three tsetses danced simultaneously, but the scent was received so strongly by the observer on all occasions that little importance can be attached to this single demonstration.

(*b*) *Hessian at* 110 *ft.* (fig. 7).

This is a coarse hempen sacking and is a material commonly employed in tsetse traps. When new it has a distinctive sweet smell. The fact that the catch of traps falls off as they become older has often been observed, and it has been suggested that the apparent decline in efficiency might be due to a loss of attractive scent. The hessian actually used was not very satisfactory, as it had been long in store, and the writer would like to repeat the experiments with fresh hessian and perhaps at a closer range. The same technique was employed as for the *kamba*, about 15 ft. of hessian being borne past the enclosure on the sledge, and it will be seen that there was no indication that it was attractive.

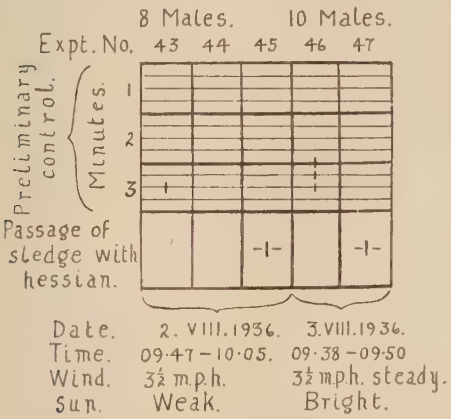


Fig. 7. Scent : Hessian at 110 ft.

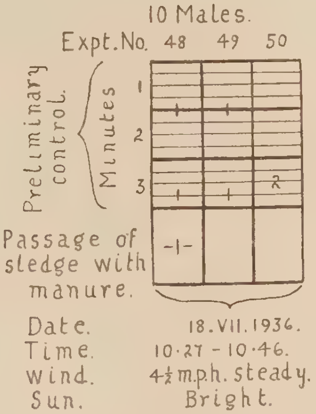


Fig. 8. Scent : Manure at 110 ft.

(*c*) *Manure at* 110 *ft.* (fig. 8).

The trial of manure was suggested by the theory that tsetses are attracted to game-paths and other places frequented by game by the scent of manure and/or the stale scent of the animals themselves. The technique used in the *kamba* experiment was once again employed, about half a bag of cattle manure—probably not more than 12 hours old—being placed on the sledge. Although the scent of the manure could be faintly detected by the observer at 110 ft. the tsetses failed to react. While these experiments indicate that manure is not attractive and Swynnerton (1933, pp. 88 and 90) found the same, yet the stale scent of game, which it is reasonable to suppose persists in their haunts, has yet to be tested. It should be added, however, that Swynnerton, in the paper referred to above, describes how a calf-trap impregnated with scent, but without the animal, was unattractive.

(*d*) *Is the Scent of the Exhaust of a Motor Vehicle attractive to Tsetses ?*

Lack of time prevented the writer from including in this paper a satisfactory series of experiments covering the surprising reaction of tsetses to the exhaust of a motor vehicle. An old 1928 model 4-cylinder Ford tourer was stopped with its engine running about 250 ft. up-wind of the scent enclosure and emitted a cloud of exhaust. The writer, standing inside the enclosure to leeward of the cage containing ten tsetses was surprised to see that as the scent of the exhaust came to him, simultaneously, in a most spectacular manner, the tsetses reacted to it. Later, for the diversion of Mr. Potts, Senior Entomologist to the Department, the writer drove his 1931 Hillman Wizard twice past the enclosure at a range of about 120 ft., and Mr. Potts standing in the enclosure observed excellent reactions. Trial experiments seemed to show that the exhaust of a brand new Bedford lorry was not as efficacious as that of the older cars—although its scent could easily be detected by the writer. Was the extra oil burnt by the older cars responsible for the superior attraction of the exhaust, or was it merely a question of the quality of exhaust ?

A group of five experiments are reproduced in fig. 9. Unfortunately only five tsetses were available and the small number detracts from the results. But together with the numerous observations of the writer they present a considerable body of evidence that under certain conditions the scent of exhaust is attractive. The writer refrains from indulging in the interesting speculations which could be built on this conclusion.

(*e*) *The Exhaust of a Lorry at* 300 *ft.* (fig. 9).

The lorry was an old 4-cylinder Chevrolet—probably 1928 model—with the engine much worn and therefore with a heavy exhaust.

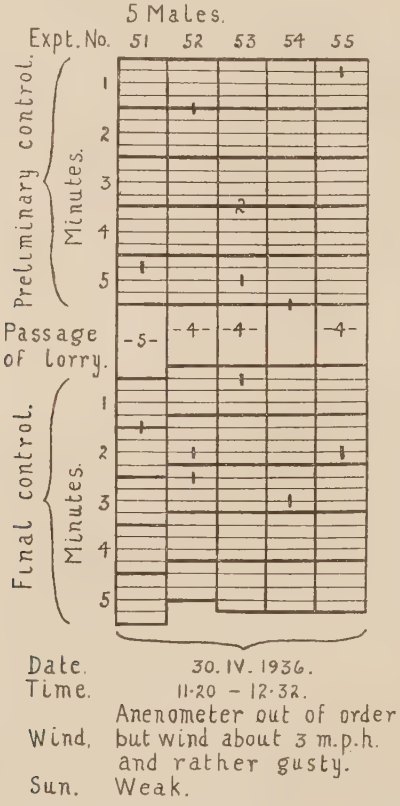


Fig. 9. Scent: Exhaust of Lorry at 300 ft.

The technique differed slightly from that followed in the oxen scent experiments, for the Passage of Lorry Period was timed from when the engine was started at C (fig. 1) to a quarter-minute after the arrival of the lorry at G. The quarter-minute was included at the end of the run to allow for the lag in the arrival of the exhaust. This protracted the Passage of Lorry Period unduly and an improved plan would be adopted were the experiments repeated.

The ground was so rough that it was impossible to change up into top-gear in the short run available. The lorry probably traversed the crucial part of the course, *i.e.*, the ox arc, at about 18 m.p.h. (the speedometer was broken) and was in second gear. It is noteworthy that the tsetses took no notice of the rattle of the empty body as it passed and only reacted on the arrival of the scent much later, which in every case (except Experiment 54, when the wind dropped) was detected by the observer. An analysis of the kind of movement that took place is given in Appendix A.

7. Discussion of the Scent Experiments.

These experiments were designed to show whether increased activity of the tsetses took place in the period in which it was possible for them to receive the scent of the oxen and men. In view of the observations on sounds, and the fact that the oxen and men were out of sight, if there were increased activity, it could only be attributed to scent.

Figs. 2 and 3 show clearly that at the ranges of 110 and 180 ft. there was comparatively great activity in the Passage of Oxen Periods ; this disappeared at 300 ft. (fig. 4). Table I sums up the position. Here the average number of movements per minute have been worked out for all the periods at the three ranges.

TABLE I.

Scent. Comparison of Results at the Three Ranges.
Number of Movements per Minute.

Range	Preliminary Control Period	Passage of Oxen Period	Final Control Period
110 ft.	1·0	5·7	0·8
180 ,, ...	0·85	5·0	0·6
300 ,, ...	0·6	0·7	0·4

The comparatively poor results in the Passage of Oxen Period at 110 ft. are due, of course, to the inordinate length of those periods in the early experiments. Table I, however, does not bring out the significant distribution of the movements that were initiated in the Passage of Oxen Periods. It represents them as spread over the whole of those periods and misses the highly important fact that at the shorter ranges they were restricted to but a fraction of them—the fraction during which presumably (and certainly at 110 ft.) the scent arrived at the cage.

In the Passage of Oxen Periods of the experiments at 110 ft., *i.e.*, Nos. 1 to 8, 59 movements (excluding the first group in Experiment 2 and all Experiment 3 in which the scent was never detected) simultaneous with the arrival of scent were observed as opposed to only 4 (the first group in Experiment 2) before it. Reference to Appendix A shows that of these simultaneous movements there were 34 flights towards the oxen and none away from them ; 27 of these were the length of the cage. There were also 25 dances, all of which occurred at the end nearest the oxen.

In the Passage of Oxen Periods of the ten experiments at 180 ft. there were altogether 50 movements which all fall in the " simultaneous " category except 3 (1 each in Experiments 11, 13 and 16). Of these 47 simultaneous movements reference to Appendix A shows that 25 were flights towards the oxen and there was none away from them ; 21 of these flights were the length of the cage. There were also 22 dances, 18 of which occurred at the oxen end and only 4 at the observer's end.

The figures have been statistically examined with the object of finding whether there is significantly more movement in the Passage of Oxen Periods than in the Preliminary Control and Final Control Periods. Throughout the treatment of the data the level of significance chosen was that of which P=0·01. That is to say, a result of such strength as herein to be called significant would occur by chance on the average once only in more than a hundred trials.

In the case of fig. 2, fractions have been taken to the nearest minute and all halves counted as wholes. When the Passage of Oxen took more than one minute the actual number of minutes was of course taken as the period within which the movements occurred ; but for calculation of the variance it was assumed that all the movements took place in a single minute. All these tactics work against obtaining a significant result. In this case activity per minute is higher in the Passage of Oxen Periods than in the Preliminary Control and Final Control Periods. By " Student's " *t* test this is strongly significant, whereas the Preliminary Control Periods and Final Control Periods are indistinguishable.

Using the same method, the results for fig. 3 are exactly as for fig. 2, and strongly significant.

In the case of fig. 4 the results are not significant.

In order to test whether the differences in total movements in the Passage of Oxen Periods of figs. 2, 3 and 4 are significant, it has been assumed that every movement was made by a different individual tsetse in any one experiment. This appears legitimate, and is probably nearly true in any case, as most of the movements in the Passage of Oxen Periods were simultaneous. From the total tsetses used the following results are obtained :—

Figure	Moving	Not moving	Total
2	69	11	80
3	50	50	100
4	10	90	100

Applying the " Chi-squared " test in turn to 2 and 3, 3 and 4, and 2 and 4, there are strongly significant differences in every case. But as to 2 and 3 and 2 and 4 being different, there is a difficulty, because the Passage of Oxen Periods were on the average longer in 2 than in 3 or 4. But we can say that there was more movement in 3 than in 4, and therefore probably more in 2 than in 4. Anyone who doubts this can perform the same operation, but using only the numbers of tsetses moving *simultaneously* in 2 and in 4, when of course a strongly significant result will appear. The same could be done with 2 and 3, though this seems unnecessary.

In the case of figure 5 the *t* test has been applied and the same method followed as when figs. 2 and 3 were considered separately, but in this case the Preliminary Control and the Final Control Periods have been amalgamated. Activity per minute is higher in the Passage of Oxen Periods than in the other two periods combined. This is strongly significant.

In fig. 5 the number of movements is insufficient to give any result.

In the case of fig. 5, with the *t* test, there is a strongly significant result in favour of enhanced activity in the Passage of Lorry Periods.

8. How far are the Results obtained a true Index of the Powers of Scent of G. swynnertoni in its Natural Environment ?

That the wild tsetses were not unduly upset by their incarceration in the cage is indicated by the comparatively small number of reactions in the control periods, when for the most part they rested tranquilly on the sides, ends and top, but seldom the bottom. The excellent response to the scent of the oxen and men at the closer ranges also indicates normality and disposes of any objection that they were dazed by their unnatural confinement.

Truly the tsetses were shielded from the scent-bearing wind in a highly artificial and effectual manner. The impenetrable grass fence 6 ft. 6 ins. high—albeit it was leaning slightly outwards and there was a gap of 9 ins. below it—was circular in shape (calculated to deflect the wind) and together with the netting of the cage might be expected to keep off much of the wind. Experiments were carried out to test this point. After calibrating two anemometers, one was placed outside the enclosure for an hour and the other in the centre next to the cage. The following were the results :—

	Outside enclosure	Inside enclosure
Feet per minute	759	510

The anemometer from outside the enclosure was then placed inside the cage while the one that stood alongside the cage was left in position. The results over an hour were :—

	Inside enclosure	Inside cage
Feet per minute	329	208

That is to say, a wind only two-thirds of that outside the enclosure was registered in the centre of it, while inside the cage itself, this figure was further reduced by one-third. Thus the wind in the cage was only about four-ninths of the strength outside the enclosure. That is a very considerable reduction, but perhaps not inordinate when it is remembered that under ordinary natural conditions tall grass, trees and bushes would form obstructions. There would also be numerous rival visual and scent distractions. However, natural conditions can be visualised that would be much more favourable to the reception of scent, for instance those normally obtaining in the feeding-grounds and large short-grass areas where there would be little or no reduction in the velocity of the wind. Not that a very strong wind is necessarily an advantage to a hungry tsetse, indeed a wind of over a certain strength would be a disadvantage, for tsetses are well known to dislike such. The experiments seem to indicate that as long as there is some wind, however lightly it blows, the tsetses can detect the scent borne. Note in this connection Experiments 1, 2 and 3 where the wind was only 1½ m.p.h. outside the cage.

To sum up, it seems reasonable to suppose that the conditions under which the scent experiments were carried out subjected the tsetses to a handicap approximating to fairly unfavourable conditions in the natural bush. Their sense of smell failed them at between 180 and 300 ft., but it would be a mistake to conclude that under more favourable conditions they could not smell further, and what the effect would have been of a possibly more favoured source of scent (perhaps buffalo or giraffe) or a larger herd of animals is not known.

9. Sight Range Experiments with Oxen and Men.

(*a*) *General Description.*

A cage of tsetses was placed in the centre of a grass enclosure similar to that used in the scent experiments, but in this case a portion of the fence on the leeward side was cut away and moved outwards. Cattle were then led to leeward of the cage (so that their scent was not received) and came into the line of sight of the tsetses as they passed the gap, the portion of the fence that had been moved outwards forming their background (Plate XIV, fig. 2). The usual preliminary and final control periods were included. The observer—out of sight—watched the reaction of the tsetses with field-glasses through a small aperture in the enclosure.

(*b*) *The Enclosure* (fig. 10).

Again, in order that the tsetses might be exposed to as little outside disturbance as possible, the principle of a complete circular enclosure was adopted. The portion of the fence that was cut away and moved outwards (called from now onwards the " background ") was extended at each end so that from no point in the cage was anything visible but the grass fence and a few distant trees above it. The gap in the grass enclosure varied with the distance of the background. At the shortest range, *i.e.*, 70 ft. it was found convenient to parade the target oxen along a length of 75 ft. To keep that length equal at the further ranges the segment cut from the round grass enclosure was reduced. Fig. 10 illustrates this. A further point to be noted is that no gap was left beneath the fence in these experiments.

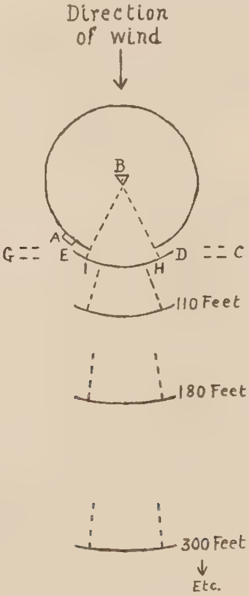


Fig. 10. Plan of sight enclosure and background.

As the grass which was used in construction was dry the enclosure was yellow-brown in colour.

(*c*) *The Sight Cage* (Plate XIII, fig. 4).

The netting cage employed in the scent experiments was tried, but it proved unsatisfactory as the tsetses apparently had great difficulty in seeing out of it. A triangular cage (24 ins. in height) was therefore made with its front consisting of two large sheets of glass set at an angle of 120° to each other and its back (41 ins. long) of netting for ventilation. Top and bottom were of wood. In order to keep the contrivance rigid it was necessary to pass an iron bar vertically through it. This in practice was not found to interfere with the view of the tsetses as they favoured a position in front of the bar. The bar and the wooden vertical side strips were chalked white to enable the tsetses to be seen. They did not apparently object to the chalk.

This cage was supported on two petrol boxes turned on end and sited in the centre of the enclosure, with the glass sides facing the background. The greatest care was taken to aim the cage correctly at the background so that tsetses at rest either on the roof or on the floor would have a clear view of the oxen.

(*d*) *The Tsetses and Oxen.*

The tsetses were collected in a similar fashion to those used in the scent experiments, and there were ten flies in each experiment.

The driver and *voorlooper* were dressed in khaki uniforms, and the same span of six black oxen was used. These oxen were purposely chosen so that they might form as great a contrast as possible to the yellow-brown of the background and thus, judged from the standard of the human eye, give the tsetses the most favourable conditions for responding.

The oxen traversed the 75 ft. of background, plus a distance equivalent to the length of the span (to allow for its disappearing), in exactly half a minute, that is to say, they moved at a pace of about two and a-quarter miles per hour.

(*e*) *The Observer* (Plate XIV, fig. 1).

The observer was seated outside the enclosure in a shelter built on one side of the gap and to leeward of the cage. A small aperture was made in the fence to take the field-glasses (Ross, power 7, field 9½). With this arrangement the movements of the tsetses could be followed with great ease. In order to test whether they would respond to any movement in the aperture, frequent efforts were made to attract their attention by moving the field-glasses and the hand, but with no response.

(*f*) *The Routine of an Experiment* (fig. 10).

B represents the cage, A the observer's shelter and DE the background. An experiment started with the oxen waiting at C out of sight and out of scent of the tsetses. Having tapped the tsetses into activity the observer retreated to his shelter and allowed them time to settle down. Then commenced the Preliminary Control Period of five minutes, just before the end of which a call was given as a signal to the driver to start with his span. As the head of the first ox passed a mark H on the background, where the tsetses could get their first view, the driver shouted and the Passage of Oxen Period had begun. When the tail of the last ox passed I, where they got their last view, he shouted again and the Passage of Oxen Period closed. Then followed the Final Control Period of five minutes with the oxen resting at G. The next experiment was carried out in the opposite direction.

(*g*) *Movement in the Sight Experiments.*

Exactly the same method was used in recording the movements of the tsetses during the sight experiments as was employed during the scent experiments, *i.e.*, movements of position, from the shortest walk to a prolonged dance, counted equally and scored 1. But as the various kinds of movement differ in significance they have been analysed in Appendix A.

(*h*) *The Diagrams.*

These follow the plan of the later scent experiments, being generally divided into four main divisions, a Preliminary Control Period of five minutes, a Passage of Oxen Period of half a minute, a Lag Period of one minute and a Final Control Period of five minutes. The Preliminary Control and Final Control Periods have been divided into half-minute periods in order that a direct comparison may be made with the half-minute of the Passage of Oxen Period, and subdivided into quarter-minutes for the sake of interest. The length of the Passage of Oxen Period always remained constant at half a minute. Movements are recorded in the periods in which they were initiated to the nearest quarter-minute, as in the scent experiments. An exception is the Passage of Oxen Period. Here there is no " floating " line and the numeral denotes simply the total number of movements that were initiated in it. Working with field-glasses made recording more difficult and division into quarter-minutes not feasible.

(*i*) *Oxen and Men at* 70 *ft.* (fig. 11).

It will be notice that this first group of experiments was carried out at a lesser range than the closest of the scent experiments, for the preliminary trial with the netting cage had given the impression that the tsetses' sight range was less than their scent range.

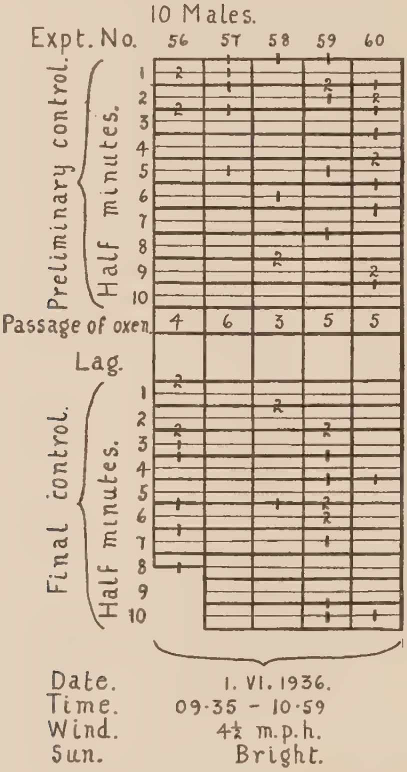


Fig. 11. Sight: 6 oxen and 2 men at 70 ft.

The five experiments were all done on one day of bright sunshine when the contrast between the black cattle and the light background should have been at its best, but it will be seen that the results were not so impressive as those of the scent experiments at the greater range of 110 ft. There is evidence in later experiments that a diminution of tonal contrast resulted in a smaller response on the part of the tsetses. That may have been responsible for the comparatively poor results in this group of experiments, for reference to fig. 10 shows that the curve of the background was at its maximum at this short range, which meant that one end tended to be thrown into semi-shadow very early as the sun rose higher and moved round. But as the background was moved further away with the increase of range so it became flatter, and unless the experiments were very protracted and lasted until late in the morning there was an excellent contrast over its entire length. This handicap was peculiar then to the shorter ranges and most serious at the shortest range of all. An attempt was made to bring out the difference in photographs, but failed.

It will not be out of place at this point to describe how the tsetses reacted to the sight of the cattle, and what is described here may be taken to apply to the remainder of the sight experiments. The top of the cage was the favourite resting place during the Preliminary Control Period, although individuals often rested on the chalked vertical side strips and occasionally on the glass front. There was seldom any reaction when the oxen first came into view, but when they were perhaps half way across the gap an individual tsetse would fly forward, strike the glass and " slither," dancing violently, to the bottom of the cage, whence it would find its way by degrees to the top once more. This tsetse would be followed sooner or later by others, but there was never the landslide—the simultaneous movement of the majority—which characterised and was so spectacular in the shorter range scent experiments. To the tsetses, of course, only three oxen were visible as the team of six were walking two abreast.

(*j*) *Oxen and Men at* 110 *ft.* (fig. 12).

Eight experiments were carried out with males and three with females. Excluding the " tailing-off " in reaction in the male experiments, the results at this range are somewhat similar to those at 70 ft. The tailing-off may perhaps be attributed in part to the fact that the male experiments lasted until nearly mid-day, when a portion of the background was in semi-shadow as already explained. Further, it is conceivable too that the tsetses tired of being " bluffed " so often and that fatigue set in.

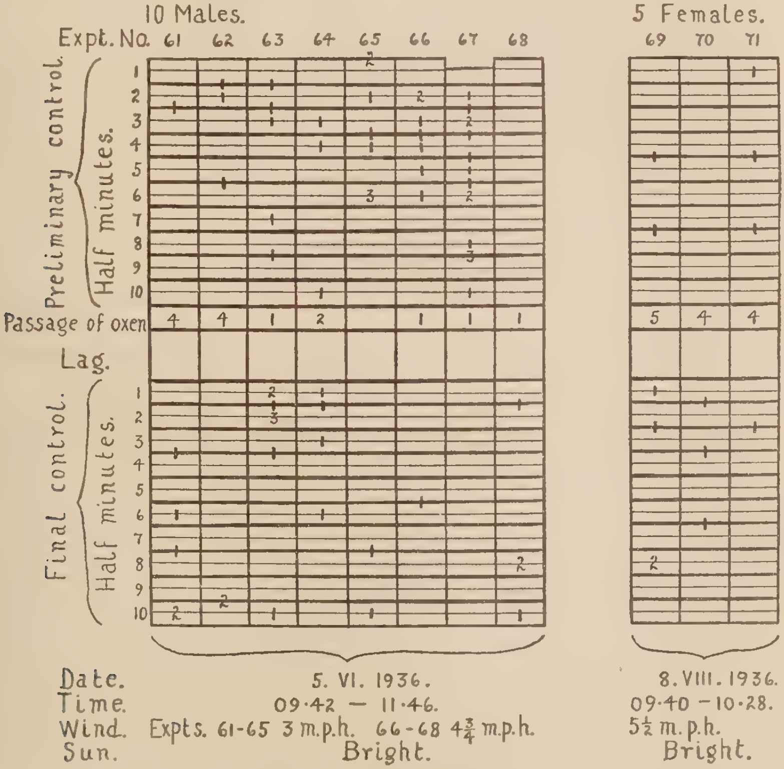
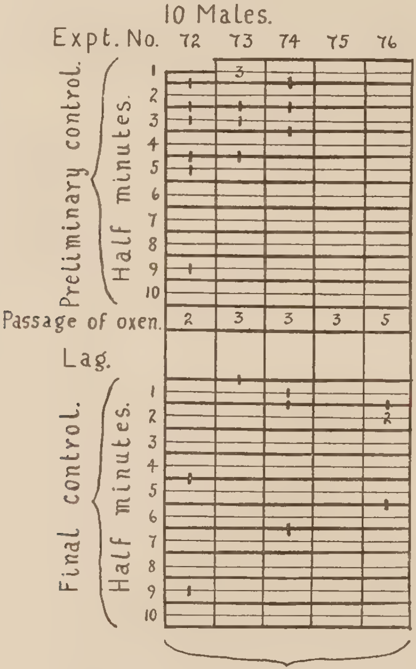


Fig. 12. Sight: 6 oxen and 2 men at 110 ft.

Only five tsetses were used in the female experiments. Because of a misjudgment on the part of the observer in Experiment 67, the Passage of Oxen Period commenced a quarter of a minute earlier than it should have done.

(*k*) *Oxen and Men at* 180 *ft.* (fig. 13).

All five experiments were carried out on the same day and in bright sun. It should be noted that this group was started considerably earlier in the morning than the 70 and 110 ft. experiments, and perhaps in that and in the fact that the background was flatter at this range, lies the explanation of the evenness and comparative excellence of the reactions.



Date. 9. VI. 1936.
Time. 09·07 – 10·20.
Wind. 6¾ m.p.h.
Sun. Bright.

Fig. 13. Sight : 6 oxen and 2 men at 180 ft.

(*l*) *Oxen and Men at* 300 *ft.* (fig. 14).

Eight experiments were carried out at this range, and it will be noticed that the group was started rather late and ended late. Reactions in the Passage of Oxen Periods were very few, but those that there were occurred in the early experiments when the sun was shining brightly. During the remaining experiments the sun was weak, and the contrast between the oxen and their background consequently poorer. It should be added that the three tsetses that danced in the Passage of Oxen Period in Experiment 79 gave the impression that they were definitely attracted by the oxen.

(*m*) *Oxen and Men at* 450 *ft.* (fig. 15).

As the limit of sight under these experimental conditions was obviously being approached, sixteen experiments were carried out at this range, the first six on a day of weak sun, the remainder on two days when the sun was bright. The negative results with the weak sun add still further evidence to the theory that lack of contrast between the oxen and their background resulted in a diminution of activity. On the other hand, with a bright sun considerable and persistent activity occurred in the Passage of Oxen Periods. It should be noted that twelve tsetses instead of the usual ten were used in the first group of experiments and eight in the second.

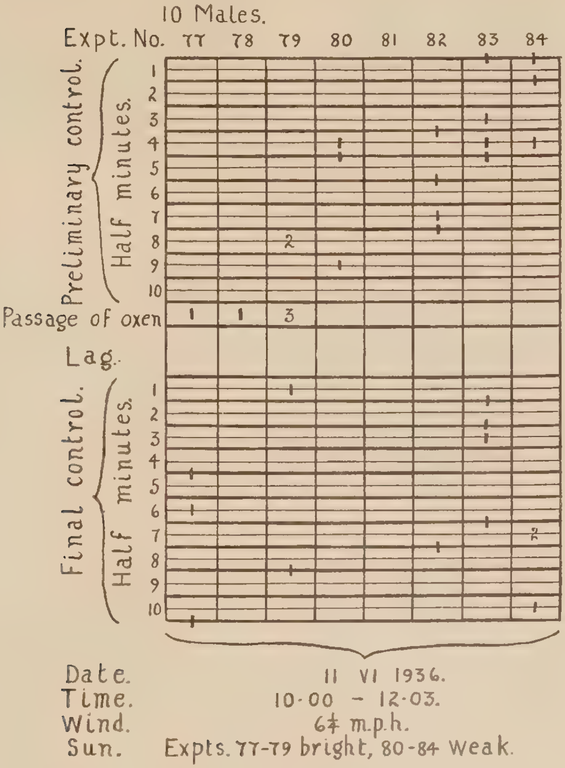


Fig. 14. Sight: 6 oxen and 2 men at 300 ft.

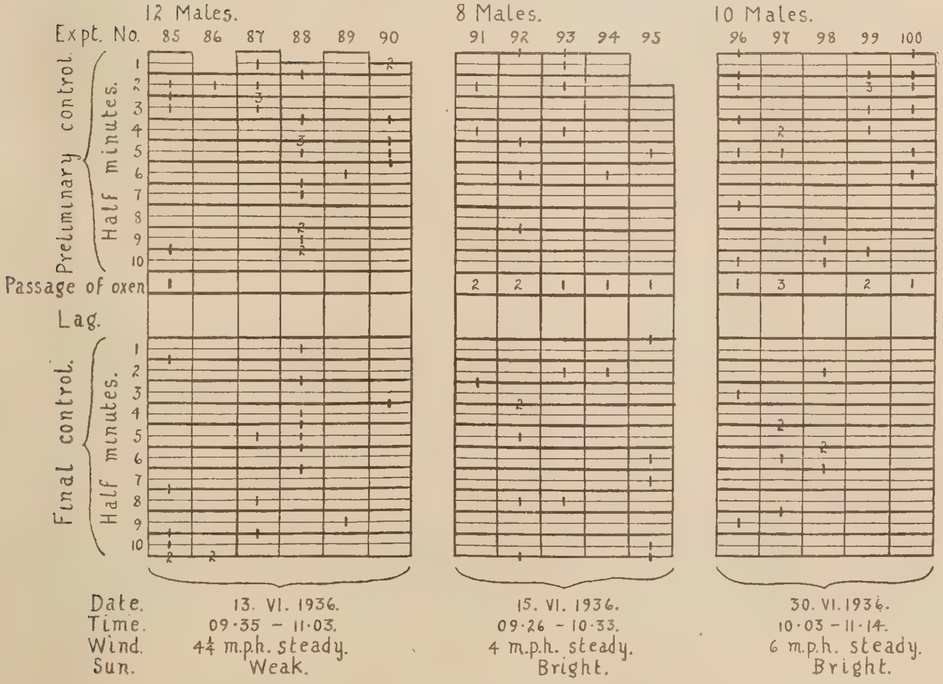


Fig. 15. Sight: 6 oxen and 2 men at 450 ft.

(*n*) *Oxen and Men at* 600 *ft.* (fig. 16).

Fifteen experiments were carried out at this range. The first five were on a day of weak sun, while the remaining ten were done in bright sunlight. It will be seen that the duller weather at this range made no difference, the reactions in the Passage of Oxen Periods of the bright days in both cases coming down to the level of those of the control periods.

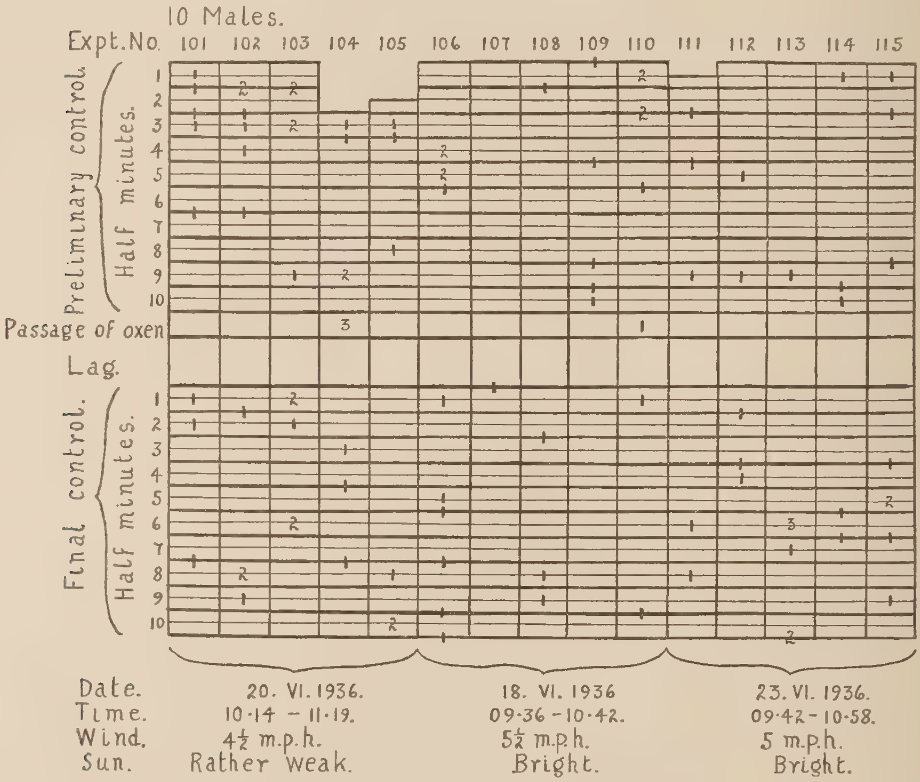


Fig. 16. Sight : 6 oxen and 2 men at 600 ft.

10. Other Sight Experiments.

(*a*) *Oxen and Men at* 110 *ft. with a light and dark Background alternately* (fig. 17).

In the experiments already described there were definite indications that a lack of contrast between the black oxen and the light-coloured background resulted in decreased response on the part of the tsetses. Such lack of contrast arose either by carrying the experiments out on a day when the sun was weaker, or by persisting in them until late in the morning when the sun was so high that part of the background, because of its curve, was thrown into semi-shadow.

To test the theory that a dark background would lead to a decrease in activity, a dark-blue cloth (black to the human eye as seen from the cage) was thrown over the grass background. Alternate experiments were then carried out, first with the black oxen passing as usual in front of the light-coloured background—the control—and then in front of the dark one. In the latter case the native driver and *voorlooper* had to strip off their clothes* to conform to the dark-colour scheme (Plate XIV, figs. 2, 3). Reference to fig. 17 shows that eight experiments (four with a light and four with a dark background) were carried out on one day of bright sunshine and six on another. Taken as a whole the results are impressive and indicate the important part played by tonal contrast.

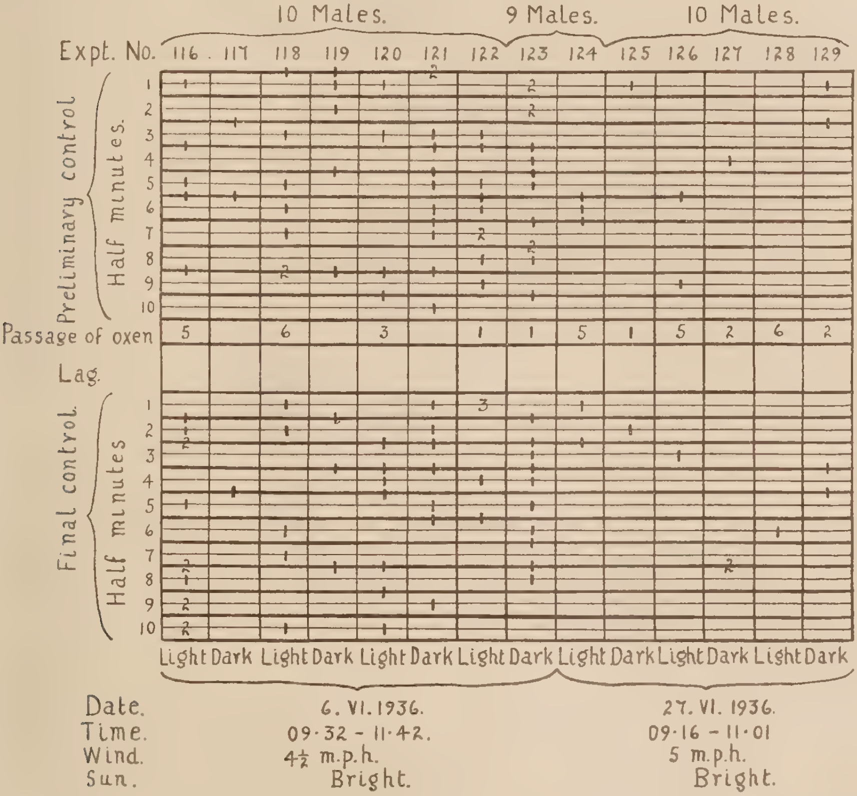


Fig. 17. Sight: 6 oxen and 2 men at 110 ft. with a light and dark background alternately.

(*b*) *A small dark screen at* 110 *ft. with light Background* (fig. 18).

In all the previous experiments a large target had been offered the tsetses. It was thought interesting therefore to try the effect of a much smaller target, but with a similar tonal contrast.

There were two objects. Firstly, to show the tsetses a target approximating the size of a small game animal and to discover their reaction to it; secondly, to

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* It will be noticed that in these photographs the heads of the natives appear above the background. Had this actually occurred during the dark background experiments, it would have diminished their value; but it did not, The greatest care was exercised and the fence was examined before the commencement of experiments for just such shortcomings as lack of height. These photographs were taken (not by the writer) actually some days after the completion of all the experiments. Natives had been sent down to repair damage done in some days of high-wind and to tidy up the grass enclosure in readiness for the photographs. They evidently patted down the top of the fence and so lessened the height, and that fact was most unfortunately not noticed at the time.

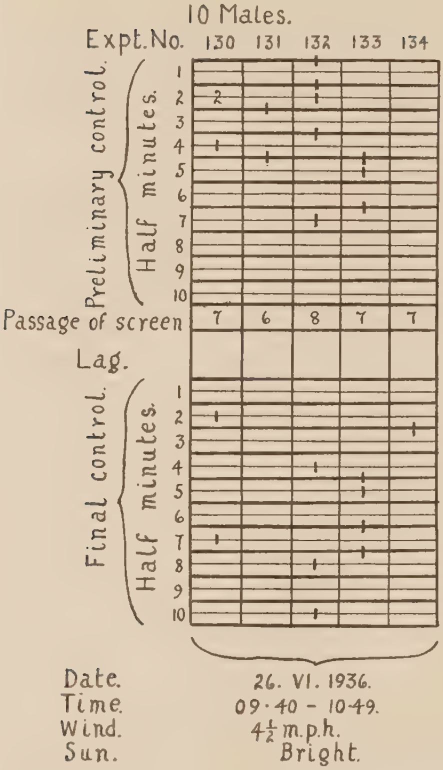

Fig. 18. Sight: small dark screen at 110 ft. with light background.

simulate the size of the team of oxen as it appeared at a long range and gain the advantage of passing it in front of a wide gap (see the discussion in Section 12) instead of a narrow one. Accordingly, a small dark screen was carried across the front of the light background at the same pace as the oxen had moved. The screen was made of the same dark-blue material as had been draped over the grass background. It measured 30 ins. by 18, but owing to the shadow thrown presented a dark object larger than its actual dimensions. A handle was attached to the screen in such a manner that the man who bore it was able to walk behind the background out of sight of the tsetses (Plate XIV, fig. 4). Reference to fig. 18 shows that the tsetses reacted strongly.

11. Discussion of the Sight Experiments.

No attempt is made here to discuss how far the experimental conditions approximated to natural ones—that question is reserved for the next section.

The sight range experiments fall naturally into two categories. Firstly, those carried out on days of bright sunshine when the contrast between the oxen and background was to human eyes at its greatest, and secondly, those done on days when the sun was weak, with a consequent diminution of contrast. Diminution of contrast occurred too when experiments were carried out late in the morning or at short ranges (with a curved background) although the sun shone brightly, but such have nevertheless been placed in the first category as it is difficult to assess the actual handicap they suffered. Because neither of these handicapping conditions were present in the majority of the experiments at the two maximum ranges (450 and 600 ft.), they do not affect the main question to be answered by Table II, *i.e.*, what was the greatest range at which the tsetses would react to the oxen?

Table II shows the number of reactions at the various ranges with a bright and with a weak sun.

TABLE II.

Sight. Comparison of the Results at the Six Ranges.
Number of Movements per Half-minute.

Range	Preliminary Control Period		Passage of Oxen Period		Final Control Period	
	Bright	Weak	Bright	Weak	Bright	Weak
70 feet	0·6	—	4·6	—	0·5	—
110 ,, ...	0·4	—	2·45	—	0·3	—
180 ,, ...	0·3	—	3·2	—	0·2	—
300 ,, ...	0·07	0·3	1·7	0·0	0·15	0·2
450 ,, ...	0·3	0·5	1·4	0·2	0·2	0·3
600 ,, ...	0·3	0·5	0·1	0·6	0·3	0·4

It will be seen that under bright conditions reactions persisted up to 450 ft., but disappeared at 600, and it would therefore appear that the limit of sight under these experimental conditions was in the neighbourhood of 500 ft. With a weak sun the tsetses did not react at even such a short range as 300 ft.

Note.—Care should be taken in comparing one range directly with another, as the control periods show that there was considerable variation in activity from day to day. On certain occasions too it will be recalled that the standard number of tsetses in an experiment—10—was departed from.

That a weak sun should cut down the range so effectively is interesting and raises the question as to what would have been the effect of a really dull day. Unfortunately time did not allow of experiments to be done to test this, but fig. 17 and Table III show how few were the reactions at this short range when the tonal contrast was very much reduced. In this connection reference must be made to the results obtained by Moggridge (1936, p. 447) when he found it inexplicable that a black ox and a white ox attracted many more tsetses than did a yellow-red ox. The oxen were standing in long green grass, and it seems probable that the lack of tonal contrast made the yellow-red ox less attractive.

TABLE III.

Sight. Comparison of Results with Light and Dark Backgrounds alternately at 110 *ft.* (*fig.* 17).
Number of Movements per Half-minute.

Background	Preliminary Control Period	Passage of Oxen Period	Final Control Period
Light	0·4	4·4	0·5
Dark	0·5	0·9	0·4

Fig. 18 has indicated that a target as small as the black screen may be attractive under certain conditions. This is interesting, as it suggests the importance of the rather smaller kinds of game to tsetses. But it must be remembered that the experiments were carried out under conditions of maximum tonal contrast and with no interference from grass and shrubs. In this connection, however, it is worth mentioning that on numerous occasions small birds were seen to fly in front of the cage, but the tsetses did not react.

As regards the simulation of distant oxen by the small screen at the short range of 110 ft., rough tests showed the screen to be about twice as high but not quite so long as the team of oxen appeared to be at 450 ft. But at 450 ft. the oxen presented a target much poorer in tonal contrast than the screen at 110 ft., owing to the effect of atmosphere, and as might be expected the reactions were very much fewer (fig. 15). Perhaps the effect may be compared with the sharp outline of the bull's-eye against its white background at 100 yards and the manner in which it seems to fade into the same background at 600.

Finally, it is of interest to note that with both targets at a range of 110 ft., and therefore under conditions of similar tonal contrast, the small black screen was at least as attractive as the far larger object presented by the oxen (figs. 12, 18).

12. How far are the Results obtained a true Index of the Powers of Sight of G. swynnertoni in its Natural Environment?

As in the net, so in the glass-fronted cage, the tsetses accepted their confinement tranquilly, and the fact that they responded to the oxen is an indication that the conditions for the purpose of the experiments approached the normal.

They were offered a black target moving across a yellow-brown monochromic background in bright sunlight. Not only was there a great contrast in colour—to the human eye at any rate—but also movement to which tsetses are specially responsive. No long grass or tree-trunks impeded their vision. In fact, but for their incarceration, conditions were as favourable to long vision as with our present knowledge they could be made.

In spite of these favourable conditions, were all the tsetses in the cage actually given a chance of seeing and responding to cattle? Could it not be that some were facing in such a direction that not even a tsetse's large eyes could detect the target? How far around can a tsetse see when at rest; is its width of vision restricted? that could account for the comparatively poor results obtained in the sight experiments as compared with those with the scent. Whatever direction a tsetse faced it might be expected to react to the scent but not so to the sight of passing oxen. Did not this gradual drawing together of the arms of the enclosure, carried out as the range increased, exclude the passing oxen from the range of vision of the border-line tsetses until finally only those directly facing the opening could hope to see the oxen at the longest ranges? But in the ten experiments carried out at 600 ft. with ten tsetses in each no response took place by any of the tsetses, favourably placed or otherwise, as judged from the controls. The view that the width of vision of a tsetse is so restricted and/or that all were so unfortunately placed as to have had no chance of seeing the oxen must be rejected. It is much more likely that the failure is a result of other limitations of a tsetse's eye. In any case, apart from the question as to how far an individual tsetse can see under optimum conditions the fact that groups of ten failed time after time to detect oxen at 600 ft. walking over so long a distance as 75 ft. is most interesting in itself. At the edges of large mbugas (seasonal swamps) they might have the opportunity of exercising any long-range sight powers they possess, but in the normal savannah bush an unobstructed view over a width of 75 ft. at a range of 200 yards is rare. Comparatively short sight would seem to serve the tsetse's purpose as usefully as long.

Finally, reference must be made once more to the colour of the target employed. Black is not one of the common colours of African animals, although shadow effects may often give that appearance. Only further experiments will reveal the reactions to greys, browns and fawns, and the effect of a dappled background.

13. Summary.

1. Male *G. swynnertoni* were placed in a cage in the middle of a grass enclosure (to curtail their sight) and their powers of smell tested by recording their reactions when a span of six oxen (with two men) passed to windward outside the enclosure. Reactions were obtained at the ranges of 110 and 180 ft. but failed at 300 ft.

Female *G. swynnertoni* reacted at 110 ft. but were not tested at greater ranges.

2. Men in groups of two and eight were substituted for the oxen, and human scent was found to be attractive, but in spite of this there was evidence that the oxen and not the men with them were the main attraction in the scent experiments with the oxen.

3. The scents of *kamba* (onion-scented bark rope), hessian and manure were tested at 110 ft. and were not attractive. There was evidence, however, that the exhaust of a lorry at 300 ft. was attractive.

4. The tsetses did not react to shouting, the trampling of oxen or the noise of a lorry.

5. These results are discussed and the experimental conditions compared with the conditions in the natural environment.

6. Wind of a strength from $1\frac{1}{2}$ to $5\frac{1}{2}$ m.p.h. outside the cage (*i.e.*, from about $\frac{3}{4}$ to $2\frac{1}{2}$ within it) successfully bore the scent of the oxen at a range of 110 ft. to the tsetses. Lower and higher velocities were not tested.

7. The powers of sight of male *G. swynnertoni* were tested by passing the span of oxen to leeward of the enclosure, from the circumference of which an arc had been cut. The direction of the wind ensured that the tsetses could receive no scent. A maximum tonal contrast was obtained (to human eyes) by using black oxen against a light background and carrying out the experiments in bright sunshine. Positive results were obtained up to and including a range of 450 ft., but at 600 ft. there was no reaction.

Female *G. swynnertoni* reacted at 110 ft. but were not tested at greater ranges.

8. There was evidence that as the tonal contrast between the oxen and their background became less (through a weak sun or the background in semi-shadow) so the distance at which the tsetses could see diminished. This was supported by an experiment at 110 ft. in which the effect of a dark-blue background was greatly to reduce the reactions.

9. A small dark screen at 110 ft. gave as good reactions as the span of oxen.

10. The results of the sight experiments are discussed and the experimental conditions compared with those in the natural environment.

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APPENDIX A.

ANALYSIS OF THE MOVEMENTS OF THE TSETSES IN THE SCENT EXPERIMENTS.

For the sake of brevity the Preliminary Control Period is hereafter referred to as the P.C.P., the Passage of Oxen Period as the P. of O. and the Final Control Period as the F.C.P.

In the diagrams, a flight—limited only by the length of the cage—and a short walk or hop, etc., counted equally as 1, with the result that the full significance of the movement might be lost. This Appendix, dealing only with those experiments in which there was increased activity during the P. of O. period, amplifies the information by showing the kind of movement that took place. But in order that the kind of movement might be rated at its proper value the position of the tsetses in the cage had to be shown ; for instance, those already situated at the oxen end of the cage at the start of the P. of O. period were precluded by that fact from registering their full reaction by flying the length of the cage towards the oxen, and could only dance instead. In order, then, that a true estimate might be formed of the difference in kind of movement and the opportunity for most spectacular movement, *i.e.*, flight, as between the control periods and the P. of O. period, the position of the tsetses in the cage has been shown as it was at (i) the opening of the P.C.P., (ii) the opening of the P. of O. and (iii) the opening of the F.C.P. Under each a summary of the movements has been shown. For ease in recording the positions of the tsetses the cage was divided approximately into three equal portions, the oxen end (shown on the left below), the middle and the observer's end.

Finally, it is necessary to add some further notes of explanation on the definition of the kinds of movements. It happened that a movement was frequently not restricted to one action only but combined two or more. In these cases the most significant action was recorded, significance being rated in the following order and this classification adopted—flight, dance, and miscellaneous (including all other movements, *e.g.* walk, hop, etc.). Common sense had sometimes to govern a decision. For instance, a protracted dance followed by a flight was counted no more than a dance, the flight being considered incidental to it, while had there been only a momentary dance or other movement before the flight, it would have counted as a flight.

At the short ranges a dance was generally engaged in by a tsetse in the P. of O. period after a flight from the observer's to the oxen end of the cage, and it appeared to be a determined attempt to continue the flight and not an idle movement. It and those tsetses already at the oxen end would often bunch together and dance in a compact group at one corner or side of the cage.

The word " simultaneous " in connection with flights means that they occurred within a period of about five seconds.

Oxen and Men at 110 *ft.*

Position of Tsetses in Cage.

	Oxen end.	*Middle*	*Observer's end.*
Experiment 1.—10 Males.			
P.C.P.	2	3	5
2 miscellaneous at observer's end.			
P. of O.	2	3	5
Simultaneously with the reception of the scent by the observer 4 flights from his end and 2 from the middle to the oxen end and at the same time the 2 already at the oxen end danced.			
F.C.P.	8	1	1
No movement.			
Experiment 2.—10 Males.			
P.C.P.	4	1	5
1 flight from oxen to observer's end. 3 dances at oxen end.			
P. of O.	3	1	6
2 dances at observer's and 2 at oxen end. Then simultaneously with reception of scent by the observer 6 flights from observer's end and 1 from middle to oxen end.			
F.C.P.	10	0	0
2 dances (as F.C.P. was ending) and 1 miscellaneous at oxen end.			
Experiment 3.—10 Males.			
P.C.P.	3	2	5
1 flight from observer's to oxen end. 1 dance at oxen end and 1 miscellaneous in middle.			
P. of O.	4	2	4
No scent detected. Lull in wind as oxen passed. Simultaneously, 1 flight from observer's and 1 from middle to oxen end, and at same time the 4 already at oxen end danced.			
F.C.P.	6	1	3
1 flight from observer's end to middle. 2 dances and 1 miscellaneous at oxen end, and 1 dance in middle.			
Experiment 4.—10 Males.			
P.C.P.	4	1	5
1 flight from observer's end to oxen end. 1 flight from observer's end to middle and 1 from middle to oxen end. 2 miscellaneous at observer's end and 1 in middle.			
P. of O.	6	1	3
Simultaneously with the reception of the scent by the observer, 2 flights from his end and 1 from the middle to the oxen end, and at same time the 6 already at oxen end danced.			
F.C.P.	9	0	1
1 dance and 1 miscellaneous at oxen end.			

Oxen and Men at 110 *ft.*—continued.

Position of Tsetses in Cage.

	Oxen end.	*Middle*	*Observer's end.*

Experiment 5.—10 Males.

P.C.P. 5 0 5

1 flight from observer's end to oxen end and 2 from his end to middle. 6 dances at oxen end, 2 of these being on border-line between the P.C.P. and P. of O. 1 miscellaneous at oxen end.

P. of O. 6 2 2

Simultaneously with the reception of scent 1 flight from observer's and 1 from middle to oxen end, and at same time the 6 already at oxen end danced.

F.C.P. 8 1 1

No movement.

Experiment 6.—10 Males.

P.C.P. 6 0 4

2 flights from observer's to oxen end and 1 from oxen end to middle. 1 miscellaneous at observer's end.

P. of O. 7 1 2

Simultaneously with the reception of scent by the observer 1 flight from his end and 1 from middle to oxen end and at same time the 7 already at oxen end danced.

F.C.P. 9 0 1

1 flight from oxen to observer's end and 2 miscellaneous at oxen end.

Experiment 7.—10 Females.

P.C.P. 2 0 8

1 flight from observer's end to middle and 1 from oxen end to observer's 5 dances at observer's end, including 1 as the P.C.P. opened. 1 miscellaneous at observer's and 1 at oxen end.

P. of O. 1 1 8

Simultaneously with the reception of scent by the observer 8 flights from his end to oxen end and at same time the 1 already at oxen end danced.

F.C.P. 9 1 0

1 flight from oxen end to observer's end and 1 from oxen end to middle. 4 dances at oxen end including 1 as F.C.P. closed. 2 miscellaneous at oxen end.

Experiment 8.—10 Females.

P.C.P. 2 1 7

1 flight from observer's to oxen end, 1 from observer's to middle and 1 from middle to observer's. 2 dances at oxen end (including 1 at the opening of the P.C.P.).

P. of O. 3 1 6

Simultaneously with the reception of the scent by the observer, 5 flights from his and 1 from middle to oxen end and at the same time the 3 already at the oxen end danced.

Oxen and Men at 110 *ft.*—continued.

Position of Tsetses in Cage.

	Oxen end.	*Middle.*	*Observer's end.*
Experiment 8.—continued.			
F.C.P.	9	0	1
1 flight from oxen end to middle and 1 from middle to observer's end. 5 dances (1 between Lag and F.C.P.) and 1 miscellaneous at oxen end.			

Oxen and Men at 180 *ft.*

Position of Tsetses in Cage.

	Oxen end.	*Middle.*	*Observer's end.*
Experiment 9.—10 Males.			
P.C.P.	1	4	5
1 flight from middle to observer's end and 1 miscellaneous at observer's end.			
P. of O.	1	3	6
Simultaneously 1 flight from observer's end and 1 from middle to oxen end.			
F.C.P.	3	2	5
1 dance at observer's end.			
Experiment 10.—10 Males.			
P.C.P.	3	1	6
1 flight from oxen to observer's end. 4 dances at observer's end.			
P. of O.	2	1	7
Simultaneously 3 flights from observer's end to oxen end, but one of these pausing in middle on its way.			
F.C.P.	5	1	4
1 dance at observer's end.			
Experiment 11.—10 Males.			
P.C.P.	1	1	8
3 dances at observer's end. 1 miscellaneous at observer's and 1 at oxen end.			
P. of O.	1	1	8
Simultaneously 2 flights from observer's to oxen end. Then 1 miscellaneous at observer's end.			
F.C.P.	3	1	6
1 dance and 1 miscellaneous at observer's end.			
Experiment 12.—10 Males.			
P.C.P.	3	2	5
1 flight from oxen end to middle and 1 from middle to observer's end. 2 dances at observer's and 1 miscellaneous at oxen end.			
P. of O.	2	2	6
Simultaneously 4 flights from observer's end and 2 from middle to oxen end, and at same time 2 already at observer's end and 2 at oxen end danced.			

Oxen and Men at 180 *ft.*—continued.

	Position of Tsetses in Cage.		
	Oxen end.	*Middle.*	*Observer's end.*
Experiment 12.—continued.			
F.C.P.	8	0	2
	1 flight from oxen end to middle. 2 dances at observer's and 1 at oxen end.		
Experiment 13.—10 Males.			
P.C.P.	2	0	8
	3 dances at observer's end 1 miscellaneous at oxen end.		
P. of O.	2	0	8
	Simultaneously 2 flights from observer's to oxen end and at the same time the 2 already at the oxen end danced. Later 1 miscellaneous at observer's end.		
F.C.P.	4	0	6
	No movement.		
Experiment 14.—10 Males.			
P.C.P.	7	1	2
	1 flight from middle to observer's end. 1 dance and 1 miscellaneous at observer's end.		
P. of O.	7	0	3
	Simultaneously 2 flights from observer's to oxen end and at same time 6 already there danced.		
F.C.P.	9	0	1
	1 dance at observer's end and 2 at oxen end (1 as F.C.P. closed). 2 miscellaneous at oxen end.		
Experiment 15.—10 Males.			
P.C.P.	3	1	6
	1 flight from middle to observer's end. 3 dances and 1 miscellaneous at observer's end.		
P. of O.	3	0	7
	Simultaneously 4 flights from observer's to oxen end and at same time the 3 already at oxen end danced.		
F.C.P.	7	0	3
	3 flights from oxen to observer's end. 1 dance at observer's and 3 at oxen end.		
Experiment 16.—10 Males.			
P.C.P.	2	1	7
	6 dances at observer's end (2 at opening of P.C.P.).		
P. of O.	2	1	7
	1 dance at oxen end. The wind was very light throughout this period.		
F.C.P.	2	1	7
	4 dances at observer's end.		

Oxen and Men at 180 *ft.*—continued.

Position of Tsetses in Cage.

	Oxen end.	*Middle*	*Observer's end.*
Experiment 17.—10 Males.			
P.C.P.	5	1	4
5 dances at observer's end (1 at opening of P.C.P.).			
P. of O.	5	1	4
Simultaneously, 2 flights from observer's end and 1 from middle to oxen end and at same time 3 already at oxen end danced.			
F.C.P.	8	0	2
3 dances at oxen end.			
Experiment 18.—10 Males.			
P.C.P.	2	1	7
1 flight from middle to observer's end and 3 dances at same end.			
P. of O.	2	0	8
1 flight from observer's to oxen end and at same time 2 dances at observer's and 2 at oxen end. Then as P. of O. period closed and the F.C.P. opened 1 miscellaneous at observer's end.			
F.C.P.	3	0	7
1 dance at oxen and 1 miscellaneous at observer's end.			

Men at 110 *ft.*

Position of Tsetses in Cage.

	Oxen end.	*Middle.*	*Observer's end.*
Experiment 29.—(2 Men.) 7 Males.			
P.C.P.	3	0	4
P. of Men			
F.C.P.			
} No movement.			
Experiment 30.—(2 Men.) 7 Males.			
P.C.P.	2	1	4
No movement.			
P. of Men	2	1	4
No movement.			
F.C.P.	2	1	4
1 flight from end nearest men to observer's end. 1 miscellaneous at observer's end.			
Experiment 31.—(8 Men.) 7 Males.			
P.C.P.	2	1	4
1 dance at observer's end.			
P. of Men	2	1	4
1 flight from observer's end to end nearest men.			

Men at 110 *ft.*—continued.

Position of Tsetses in Cage.

	Oxen end.	*Middle.*	*Observer's end.*
Experiment 31.—continued.			
F.C.P.	3	1	3
1 flight from middle to observer's end. 4 dances at observer's end and 1 miscellaneous at end nearest men.			
Experiment 32.—(2 Men.) 7 Males.			
P.C.P.	3	0	4
1 dance at observer's end.			
P. of Men	3	0	9
Simultaneously 1 dance and 1 miscellaneous at observer's end.			
F.C.P.	3	0	4
No movement.			
Experiment 33.—(8 Men.) 7 Males.			
P.C.P.	4	0	3
No movement.			
P. of Men	4	0	3
Simultaneously 2 flights from observer's end to that nearest men and at same time 1 already there danced.			
F.C.P.	6	0	1
1 dance at observer's end.			
Experiment 34.—(8 Men.) 7 Males.			
P.C.P.	5	0	2
No movement.			
P. of Men	5	0	2
Simultaneously, 2 flights from observer's end to that nearest men.			
F.C.P.	7	0	0
No movement.			
Experiment 35.—(2 Men.) 7 Males.			
P.C.P.	4	0	3
No movement.			
P. of Men	4	0	3
1 miscellaneous at end nearest men.			
F.C.P.	4	0	3
1 flight from end nearest men to observer's end and 1 dance at his end.			
Experiment 36.—(8 Men.) 7 Males.			
P.C.P.	4	0	3
No movement.			
P. of Men	4	0	3
Simultaneously 1 flight from observer's end to end nearest men and 1 miscellaneous at that end.			
F.C.P.	5	0	2
1 dance at observer's end.			

The exhaust of a Lorry at 300 *ft.*

	Lorry end.	*Middle.*	*Observer's end.*
Experiment 51.—5 Males.			
P.C.P.	1	2	2
1 miscellaneous at observer's end.			
P. of Lorry ...	1	2	2
Simultaneously with the reception of the scent by the observer 1 flight from his end and 2 from middle to lorry end, and the 1 already at lorry end danced. 1 miscellaneous at observer's end. In the latter part of its movement 1 travelled back from lorry end to middle.			
F.C.P.	3	1	1
1 miscellaneous at lorry end.			
Experiment 52.—5 Males.			
P.C.P.	2	1	2
1 miscellaneous at observer's end.			
P. of Lorry ...	2	1	2
Simultaneously with the reception of the scent by the observer 1 flight from his and 1 from middle to lorry end and at the same time the 2 already there danced. Then in the latter parts of their movements 2 returned, 1 to middle and 1 to observer's end.			
F.C.P.	2	1	2
1 flight from lorry to observer's end and return. 1 miscellaneous at observer's end.			
Experiment 53.—5 Males.			
P.C.P.	3	1	1
1 flight from lorry end to observer's end and 1 from middle to lorry end. 1 miscellaneous at observer's end.			
P. of Lorry ...	3	0	2
Simultaneously with reception of the scent by the observer, 1 flight from his to lorry end and at the same time the 3 already there danced.			
F.C.P.	4	0	1
1 flight from lorry to observer's end.			
Experiment 54.—5 Males.			
P.C.P.	3	0	2
As P.C.P. closed and P. of Lorry opened, 1 dance at observer's end.			
P. of Lorry ...	3	0	2
No movement beyond that indicated in the P.C.P. There was a lull in the wind as the lorry passed.			
F.C.P.	3	0	2
1 miscellaneous at observer's end.			

The exhaust of a Lorry at 300 *ft.*—continued.

	Lorry end.	*Middle.*	*Observer's end.*
Experiment 55.—5 Males.			
P.C.P.	4	0	1
1 dance at observer's end.			
P. of Lorry ...	4	0	1
Simultaneously with the reception of scent by the observer, 1 flight from his end to lorry end and at the same time 3 already there danced. Then at latter end of its movement 1 returned to observer's end.			
F.C.P.	4	0	1
1 dance at lorry end.			

APPENDIX B.

Analysis of the Movements of the Tsetses in the Sight Experiments.

Space was so restricted in the cage used in the sight experiments that there was little scope for flight, and that kind of movement therefore was difficult to differentiate from a dance. Consequently flight does not figure as a "separate movement" in these experiments, only two kinds of movement being recorded, *viz.*, dance and miscellaneous. With the abolition of flight, the position the tsetses took up in the cage at the opening of each period is not of sufficient importance to record here—particularly as the cage was so shaped that they could only be shown as sitting at the left or right side (as seen by the observer) and not closer to or further away from the oxen.

Oxen and Men at 70 *ft.*

Experiment 56.—10 Males.
P.C.P. ... ... 3 dances and 1 miscellaneous.
P. of O. ... ... 4 danced.
F.C.P. ... ... 4 dances and 5 miscellaneous (1 as F.C.P. closed). Due to an interruption this period was $1\frac{1}{4}$ minutes short.

Experiment 57.—10 Males.
P.C.P. ... ... 4 dances (1 as P.C.P. opened) and 1 miscellaneous.
P. of O. ... ... 6 danced.
F.C.P. ... ... No movement.

Experiment 58.—10 Males.
P.C.P. ... ... 2 dances and 2 miscellaneous (1 as P.C.P. opened).
P. of O. ... ... 3 danced.
F.C.P. ... ... 2 dances and 1 miscellaneous.

Experiment 59.—10 Males.
P.C.P. ... ... 2 dances and 4 miscellaneous (1 as P.C.P. opened).
P. of O. ... ... 5 danced.
F.C.P. ... ... 6 dances and 5 miscellaneous.

Oxen and Men at 70 *ft.*—continued.

Experiment 60.—10 Males.
P.C.P. ... ... 4 dances and 8 miscellaneous.
P. of O. ... ... 5 danced.
F.C.P. ... ... 2 miscellaneous.

Oxen and Men at 110 *ft.*

Experiment 61.—10 Males.
P.C.P. ... ... 1 miscellaneous.
P. of O. ... ... 4 moved, probably 2 danced and 2 miscellaneous, but could not be accurately observed.
F.C.P. ... ... 1 dance and 4 miscellaneous.

Experiment 62.—10 Males.
P.C.P. ... ... 2 dances and 1 miscellaneous.
P. of O. ... ... 4 moved, probably 2 danced and 2 miscellaneous, but could not be accurately observed.
F.C.P. ... ... 2 dances.

Experiment 63.—10 Males.
P.C.P. ... ... 2 dances and 3 miscellaneous.
P. of O. ... ... 1 danced.
F.C.P. ... ... 8 miscellaneous.

Experiment 64.—10 Males.
P.C.P. ... ... 1 dance and 2 miscellaneous.
P. of O. ... ... 2 danced.
F.C.P. ... ... 3 dances and 1 miscellaneous.

Experiment 65.—10 Males.
P.C.P. ... ... 4 dances and 4 miscellaneous (2 of these as P.C.P. opened).
P. of O. ... ... No movement.
F.C.P. ... ... 1 dance and 1 miscellaneous.

Experiment 66.—10 Males.
P.C.P. ... ... 7 miscellaneous.
P. of O. ... ... 1 miscellaneous.
F.C.P. ... ... 1 miscellaneous.

Experiment 67.—10 Males.
P.C.P. ... ... 1 dance and 14 miscellaneous.
P. of O. ... ... 1 miscellaneous.
F.C.P. ... ... No movement.

Experiment 68.—10 Males.
P.C.P. ... ... No movement.
P. of O. ... ... 1 miscellaneous.
F.C.P. ... ... 1 dance and 3 miscellaneous.

Oxen and Men at 110 *ft.*—continued.

Experiment 69.—5 Females.
P.C.P. ... ... 2 dances.
P. of O. ... ... 5 danced.
F.C.P. ... ... 4 dances.

Experiment 70.—5 Females.
P.C.P. ... ... No movement.
P. of O. ... ... 4 danced.
F.C.P. ... ... 2 dances and 1 miscellaneous.

Experiment 71.—5 Females.
P.C.P. ... ... 3 dances.
P. of O. ... ... 4 danced.
F.C.P. ... ... 1 miscellaneous.

Oxen and Men at 180 *ft.*

Experiment 72.—10 Males.
P.C.P. ... ... 2 dances and 4 miscellaneous.
P. of O. ... ... 2 danced.
F.C.P. ... ... 1 dance and 1 miscellaneous.

Experiment 73.—10 Males.
P.C.P. ... ... 2 dances and 4 miscellaneous.
P. of O. ... ... 3 danced.
F.C.P. ... ... 1 dance.

Experiment 74.—10 Males.
P.C.P. ... ... 3 dances.
P. of O. ... ... 3 danced.
F.C.P. ... ... 3 dances.

Experiment 75.—10 Males.
P.C.P. ... ... No movement.
P. of O. ... ... 3 danced.
F.C.P. ... ... No movement.

Experiment 76.—10 Males.
P.C.P. ... ... No movement.
P. of O. ... ... 5 danced.
F.C.P. ... ... 4 dances.

Oxen and Men at 450 *ft.*

Experiment 91.—8 Males.
P.C.P. ... ... 1 dance and 1 miscellaneous.
P. of O. ... ... 2 danced.
F.C.P. ... ... 1 dance.

Oxen and Men at 450 *ft.*—continued.

Experiment 92.—8 Males.
P.C.P. ... ... 3 dances (1 of these at opening of P.C.P.) and 1 miscellaneous.
P. of O. ... ... 2 danced.
F.C.P. ... ... 1 dance and 4 miscellaneous (1 of these as F.C.P. closed).

Experiment 93.—8 Males.
P.C.P. ... ... 2 dances and 2 miscellaneous (1 of these as P.C.P. opened).
P. of O. ... ... 1 danced.
F.C.P. ... ... 2 dances.

Experiment 94.—8 Males.
P.C.P. ... ... 1 dance.
P. of O. ... ... 1 miscellaneous. It was not thought that this tsetse had been attracted by the oxen.
F.C.P. ... ... 1 dance.

Experiment 95.—8 Males.
P.C.P. ... ... 1 dance.
P. of O. ... ... 1 miscellaneous.
F.C.P. ... ... 4 dances (1 of these as the F.C.P. was closing) and 1 miscellaneous.

Experiment 96.—10 Males.
P.C.P. ... ... 3 dances and 4 miscellaneous (1 of these as the P.C.P. opened).
P. of O. ... ... 1 danced.
F.C.P. ... ... 1 dance and 1 miscellaneous.

Experiment 97.—10 Males.
P.C.P. ... ... 3 dances.
P. of O. ... ... 3 danced.
F.C.P. ... ... 4 dances.

Experiment 98.—10 Males.
P.C.P. ... ... 2 dances.
P. of O. ... ... No movement.
F.C.P. ... ... 1 dance and 3 miscellaneous.

Experiment 99.—10 Males.
P.C.P. ... ... 6 dances and 1 miscellaneous.
P. of O. ... ... 2 danced.
F.C.P. ... ... No movement.

Experiment 100.—10 Males.
P.C.P. ... ... 4 dances (1 of these as the P.C.P. opened) and 2 miscellaneous.
P. of O. ... ... 1 danced.
F.C.P. ... ... No movement.

Oxen and Men at 110 *ft. with a Light and Dark Background alternately.*

Experiment 116.—(Light Background). 10 Males.
P.C.P. ... ... 1 dance and 4 miscellaneous.
P. of O. ... ... 5 danced.
F.C.P. ... ... 12 miscellaneous.

Experiment 117.—(Dark Background). 10 Males.
P.C.P. ... ... 2 dances.
P. of O. ... ... No movement.
F.C.P. ... ... 1 miscellaneous.

Experiment 118.—(Light Background.) 10 Males.
P.C.P. ... ... 3 dances (1 of these as P.C.P. opened) and 4 miscellaneous.
P. of O. ... ... 6 danced.
F.C.P. ... ... 4 dances and 1 miscellaneous.

Experiment 119.—(Dark Background.) 10 Males.
P.C.P. ... ... 2 dances and 3 miscellaneous (1 of them as P.C.P. opened).
P. of O. ... ... No movement.
F.C.P. ... ... 3 dances.

Experiment 120.—(Light Background.) 10 Males.
P.C.P. ... ... 2 dances and 2 miscellaneous.
P. of O. ... ... 3 danced.
F.C.P. ... ... 4 dances and 3 miscellaneous.

Experiment 121.—(Dark Background.) 10 Males.
P.C.P. ... ... 3 dances and 8 miscellaneous (2 of them as P.C.P. opened).
P. of O. ... ... No movement.
F.C.P. ... ... 6 dances and 1 miscellaneous.

Experiment 122.—(Light Background.) 10 Males.
P.C.P. ... ... 3 dances and 6 miscellaneous.
P. of O. ... ... 1 danced.
F.C.P. ... ... 1 dance and 4 miscellaneous.

Experiment 123.—(Dark Background.) 9 Males.
P.C.P. ... ... 6 dances and 7 miscellaneous.
P. of O. ... ... 1 miscellaneous, but this tsetse is not thought to have reacted to the sight of the oxen.
F.C.P. ... ... 3 dances and 7 miscellaneous.

Experiment 124.—(Light Background.) 9 Males.
P.C.P. ... ... 3 miscellaneous.
P. of O. ... ... 5 danced.
F.C.P. ... ... 1 dance and 1 miscellaneous.

Experiment 125.—(Dark Background.) 10 Males.
P.C.P. ... ... 1 miscellaneous.
P. of O. ... ... 1 danced.
F.C.P. ... ... 1 dance.

Oxen and Men at 110 *ft. with a Light and Dark Background alternately.*—continued.

Experiment 126.—(Light Background.) 10 Males.
P.C.P. ... ... 2 dances.
P. of O. ... ... 5 danced.
F.C.P. ... ... 1 dance.

Experiment 127.—(Dark Background.) 10 Males.
P.C.P. ... ... 1 miscellaneous.
P. of O. ... ... 2 danced.
F.C.P. ... ... 2 dances.

Experiment 128.—(Light Background.) 10 Males.
P.C.P. ... ... No movement.
P. of O. ... ... 6 danced.
F.C.P. ... ... 1 miscellaneous.

Experiment 129.—(Dark Background.) 10 Males.
P.C.P. ... ... 2 dances.
P. of O. ... ... 2 danced.
F.C.P. ... ... 1 dance and 1 miscellaneous.

Small Dark Screen at 110 *ft. with Light Background.*

Experiment 130.—10 Males.
P.C.P. ... ... 2 dances and 1 miscellaneous.
P. of Screen ... 7 danced.
F.C.P. ... ... 2 miscellaneous.

Experiment 131.—10 Males.
P.C.P. ... ... 1 dance and 1 miscellaneous.
P. of Screen ... 6 danced.
F.C.P. ... ... No movement.

Experiment 132.—10 Males.
P.C.P. ... ... 1 dance and 4 miscellaneous (1 of these as P.C.P. opened).
P. of Screen ... 8 danced.
F.C.P. ... ... 3 dances.

Experiment 133.—10 Males.
P.C.P. ... ... 2 dances and 1 miscellaneous.
P. of Screen ... 7 danced.
F.C.P. ... ... 3 dances and 1 miscellaneous.

Experiment 134.—10 Males.
P.C.P. ... ... No movement.
P. of Screen ... 7 danced.
F.C.P. ... ... 1 miscellaneous.

APPENDIX C.

Disturbance of Inactive by Active Tsetses.

With tsetses confined in so small a space as a cage there must always be a certain amount of disturbance of the would-be quiescent by the more active, even with the sexes separated. Examples of this, both in the scent and sight experiments, were not infrequently observed.

It might be objected that in the scent experiments tsetses flying from the observer's end would disturb those already at the oxen end of the cage and this was undoubtedly so on occasions. But if such disturbance did in fact take place on any large scale it would have been equally true of all three periods and would merely have given an exaggerated picture of general activity—not have altered the intensity of activity in one period as compared with another. Thus the results of the experiments would have been the same.

Explanation of Plate XIII.

Fig. 1.—The scent enclosure with sight enclosure in distance.
Fig. 2.—The scent cage and observer.
Fig. 3.—The sledge.
Fig. 4.—The sight cage.

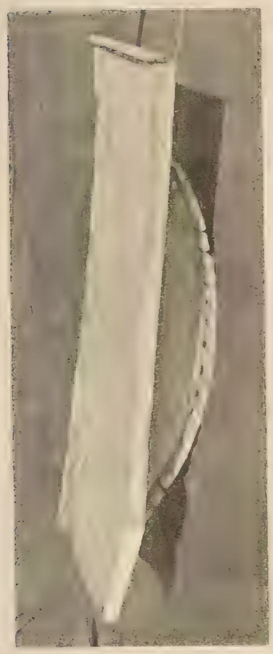

Fig. 3.

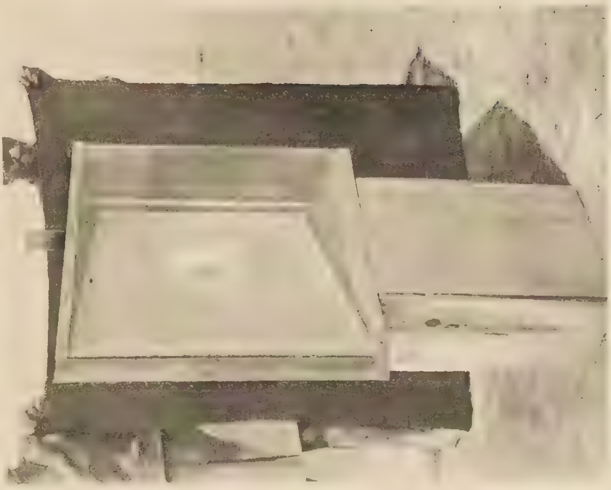

Fig. 4.

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Fig. 1.

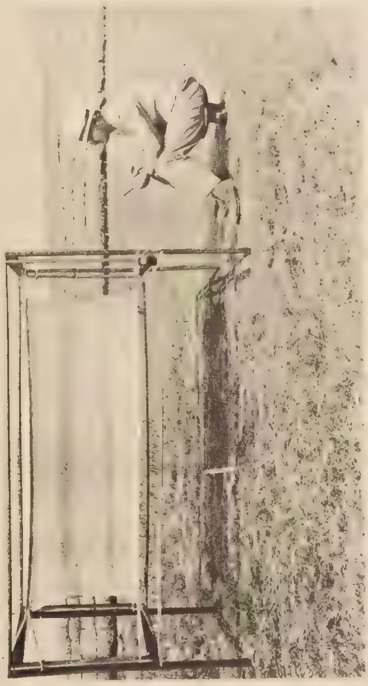

Fig. 2.

EXPLANATION OF PLATE XIV.

Fig. 1.—The observer in the sight experiments.
Fig. 2.—The span of oxen at 110 ft. with light background.
Fig. 3.—The span of oxen at 110 ft. with dark background.
Fig. 4.—The dark screen at 110 ft. with light background.

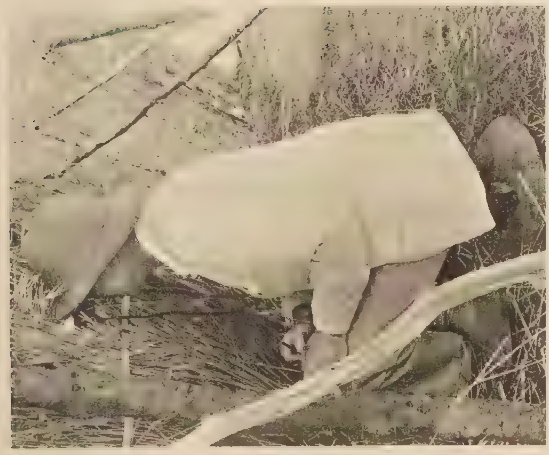

Fig. 1.

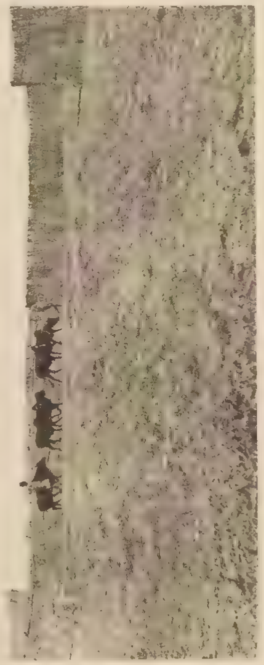

Fig. 2.

Fig. 3.

Fig. 4.

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THE MOSQUITOS OF THE *FUNESTUS* SERIES IN EAST AFRICA.

By H. S. Leeson,
London School of Hygiene & Tropical Medicine.

(Plates XV and XVI.)

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Introduction.

The exact identification of *Anopheles funestus* has been a matter of some difficulty and doubt owing to the existence of closely related Anophelines. Variations in wing ornamentation among the series were described by the author (1930 *b*) from material collected in Southern Rhodesia. Other forms found in South Africa were recorded by De Meillon (1933). Some allied forms have recently been treated as distinct species or varieties by Leeson (1930*a* and 1935), Evans (1931), and Evans & Leeson (1935) from material bred in Southern Rhodesia, and by Evans & Garnham (1936) from material bred in Kenya. More recently Evans & Leeson (1937) have recorded a form of *A. rivulorum* which is widely distributed in East Africa.

The writer visited East Africa in 1936 for the purpose of continuing the study of these mosquitoes under instructions from the London School of Hygiene and Tropical Medicine. Material was collected in Uganda, Tanganyika and in the islands of Zanzibar and Pemba during the period February to October.

Besides the taxonomy of the series certain aspects of bionomics were also studied. The light at breeding-places was recorded, house-frequenting habits were noted, a number of females were dissected for examination for malaria parasites, and the presence or absence of human blood in the gut was investigated by the precipitin test. It will be understood that the observations made and the conclusions arrived at as a result of the investigation will apply only to those places and at those times where and when the work was done.

Acknowledgments.

I wish to place on record my sincere appreciation of the work performed by Mr. J. D. Gillett, formerly of the junior staff of the Department of Entomology of the School, who accompanied me as my assistant. His intelligent and painstaking work, coupled with reliability and an intense interest in the objects of the investigation, was from start to finish a source of great satisfaction to me.

The precipitin tests were kindly carried out by Mr. C. B. Symes and his staff of the Department of Entomology in the Medical Research Laboratory, Nairobi, Kenya, to whom my best thanks are due.

Transport facilities and concessions by the various Governments in East Africa are gratefully acknowledged, also many personal courtesies rendered by Government officials and others throughout the country.

Finally, I wish to record my thanks to Professor W. W. Jameson, Dean of the London School of Hygiene and Tropical Medicine, and to Professor P. A. Buxton, Director of the Department of Entomology at the School, for the opportunity of investigating this intensely interesting and important group of *Anopheles* mosquitoes.

Methods.

At first it was intended to make the laboratory at Entebbe the headquarters and to do the first collecting around there and Kampala, 25 miles away; but this was soon abandoned owing to the scarcity of material. Next, Tororo in the east of Uganda was chosen as a base, but after twelve days the number of specimens available was so disappointing that I returned to Entebbe. I then equipped myself for a prolonged journey, intending to search the country for places which would yield sufficient *funestus* material for my purpose. This was the method finally adopted and adhered to throughout the tour. The search for *A. funestus* was continuous; if it was found, a few days were spent in the place; if it was not, records were completed and the expedition moved on. About 10,000 miles were travelled by motor-car and a few hundreds by railway and steamship; in addition, the work itself entailed much walking.

Field Work.

On arriving at a watercourse, pool or swamp, light readings were recorded whether larvae were obtained or not; identifications of any larvae collected were left till later. Larvae were put into numbered tubes in the water in which they were collected. Huts and houses were visited and cleared of adult Anophelines both by day and by night. All collecting of larvae and adults was done by or under the immediate supervision of Mr. Gillett or myself.

Laboratory Work.

The day's catch was examined on returning to camp. Some larvae and pupae were isolated and later the larval and pupal pelts and the emerged adults were preserved. Other larvae and pupae were preserved in formal glycerine (formalin 5 parts, glycerine 2 parts, water 93 parts).

Some of the adults caught were pinned, the glands and stomachs of others were examined for malaria parasites; the heads and wings of these were preserved. The stomachs of females containing blood were expressed on to filter paper ready for the precipitin tests, the glands of these were examined and their heads and wings preserved. Females containing eggs were put aside for egg-laying; they and their eggs were preserved. In many instances, the glands and stomachs of egg-layers were examined, in these cases the heads and wings were preserved also.

On returning to England a portion of the preserved material, both bred and collected, which had been put aside for further examination was studied in detail.

This material consisted largely of larval pelts, pharyngeal armatures and wings. A long series of wings and larval pelts was examined and about 120 pharyngeal armatures.

Members of the *funestus* series found to occur in E. Africa were *Anopheles funestus*, Giles, type form, *A. leesoni*, Evans, *A. rivulorum*, Leeson, and a new form *A. rivulorum* var. *garnhamellus*, Evans & Leeson, recently described (Evans & Leeson 1937). Distinguishing characters of the wings of these forms are shown in Table I ; the main larval characters are given in Table II.

Anopheles funestus, Giles.

Bred Material.

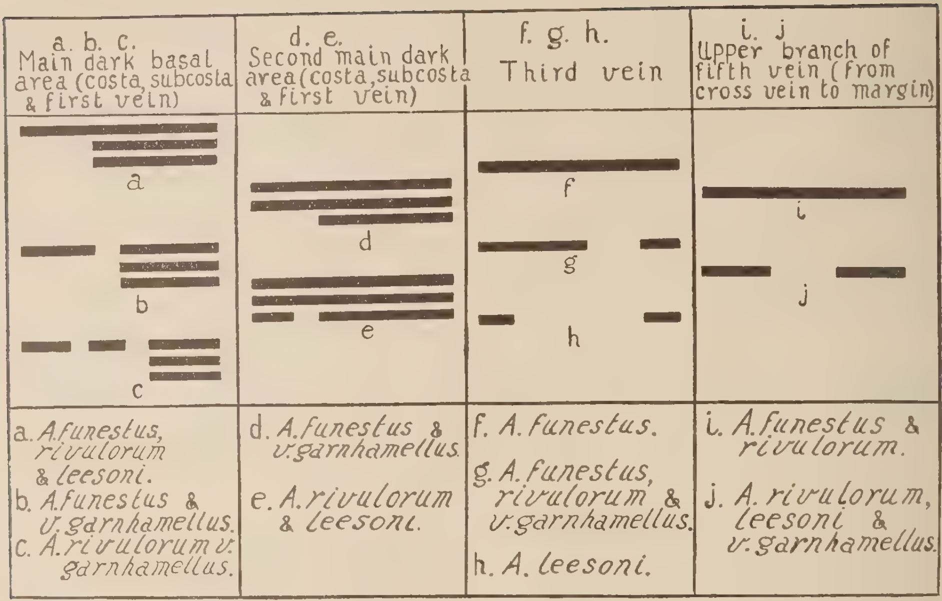
Larvae provisionally identified as *A. funestus* were isolated. In due course 137 larval and pupal pelts and their respective adults were obtained. Microscopical examination of the pelts confirmed the identification. All were of the type form as described by Evans & Leeson (1935). The identification was further corroborated by examination of 20 pharyngeal armatures and a few male terminalia.

Examination of the wings of the bred adults showed that there were four distinct variations in the pattern (Table I and fig. 1). It was discovered that, though the dark area at the base of the costa may or may not be interrupted by one pale spot and the third vein may or may not be all dark, there were two constant features about these characters. Firstly, when the base of the costa was interrupted it was by one pale spot only ; and secondly, when pale scales were present on the third vein they were mainly situated beyond the middle point. Two other constant characters were noticed. The most important of these was the *absence of a dark preaccessory sector spot on vein one opposite the proximal end of the second dark costal spot.* The other was that the upper branch of vein 5 was always completely dark. A minor variation was observed in two specimens ; in these, the first two main dark costal spots were fused at the front edge of the wing. This can be regarded as an aberration.

TABLE I.

Table of wing characters of the funestus *series occurring in East Africa.*

Wing group	Dark area at base of costa	Dark pre-accessory sector spot on vein 1 opposite proximal end of 2nd main dark costal spot	3rd vein	Upper branch of 5th vein from cross-vein to margin	Species
1	uninterrupted	absent	pale beyond middle	all dark	*funestus*
2	,,	,,	all dark	,, ,,	
3	interrupted by one pale area	,,	pale beyond middle	,, ,,	
4	interrupted by one pale area	,,	all dark	,, ,,	
1	uninterrupted	present	pale beyond middle	pale area	*rivulorum*
2	,,	,,	,, ,,	all dark	
3	,,	,,	all dark	,, ,,	
	uninterrupted	present	pale area extensive	all dark	*leesoni*
1	interrupted by one pale area	absent	pale area beyond middle	pale area	*rivulorum* var. *garnhamellus*
2	interrupted by two pale areas	,,	,, ,,	,, ,,	



a. b. c. Main dark basal area (costa, subcosta & first vein)	d. e. Second main dark area (costa, subcosta & first vein)	f. g. h. Third vein	i. j Upper branch of fifth vein (from cross vein to margin)
a. *A. funestus, rivulorum & leesoni.* b. *A. funestus & v. garnhamellus.* c. *A. rivulorum v. garnhamellus.*	d. *A. funestus & v. garnhamellus.* e. *A. rivulorum & leesoni.*	f. *A. funestus.* g. *A. funestus, rivulorum & v. garnhamellus.* h. *A. leesoni.*	i. *A. funestus & rivulorum.* j. *A. rivulorum, leesoni & v. garnhamellus.*

Fig. 1. Diagrammatic representation of the main wing characters of the *funestus* series of *Anopheles* as seen in East Africa. The base of the wing is assumed to be to the left of each diagram; areas of pale scales are blank.

TABLE II.

Table of larval characters of the funestus *series occurring in East Africa.*

Fronto-clypeal markings	Post-frontal hairs	Tergal plates	Accessory plates	Species
anterior transverse band	simple or bifid	large, deep	3 on main plate	*A. funestus*
anterior transverse band	3 or more branches	very shallow back to front	3 off main plate	*A. rivulorum*
paired longitudinal stripes or areas	3 or more branches	shallow back to front	1 on main plate; 2 off main plate	*A. leesoni*
anterior transverse band often very broad	3 or more branches	very shallow back to front	1 only, off main plate	*A. rivulorum* var. *garnhamellus*

137 bred adults were examined and the numbers occurring in each wing group were as follows :—

Wing group	*Number*	*Percentage*
1	74	54
2	21	15
3	37	27
4	5	4
	137	100

Bred specimens from Pemba and Zanzibar numbered 12 (6 from each island) and all had wings of the third type. There were 2 only from Tanga and both had the third type of wing. Out of 11 specimens from Dar-es-Salaam 7 were of this type. Kilosa, Morogoro and Shinyanga (inland towns) provided 86 bred specimens, of which number the majority were of the first type. 24 specimens from Uganda were all of the first type. There seemed to be some relationship between wing forms and geographical distribution.

Caught Material.

In order to test this, more than 1,400 specimens identified as *A. funestus* were taken at random and nearly 100 pharyngeal armatures were dissected out. Examina-

TABLE III.

Number of pairs of wings of A. funestus *examined and the percentages present in each wing group Figures for group* 1 *arranged in order of magnitude.*

District	Pairs of wings examined	Percentages present			
		Group 1	Group 2	Group 3	Group 4
Zanzibar Protectorate					
Pemba	60	7	0	83	10
Zanzibar	183	15	0	83	2
Tanganyika					
Kilosa	45	31	38	20	11
Tinde	67	33	63	0	4
Tanga	73	38	8	46	8
Dar-es-Salaam	292	48	12	34	6
Shinyanga	64	56	27	13	4
Morogoro	89	61	19	16	4
Moshi	11	64	9	18	9
Mwanza	83	64	31	5	0
Uganda					
Ajumani	10	70	30	0	0
Chabahinga	151	74	24	2	0
Rhino Camp	55	75	18	7	0
Pakwach	21	76	19	5	0
Abbia	20	80	10	10	0
Muko	143	81	17	2	0
Lira	65	82	14	4	0
Soroti	40	88	10	2	0
Mbale	81	95	1	4	0

tion of these and of a few male terminalia confirmed the identification. The wings were then examined and the four wing forms separated. The percentages falling into each group were calculated and the names of the localities from which the specimens came were added. On arranging the percentages falling into the first group in order of magnitude it was found that the places were automatically grouped according to countries. Even the addition of the figures for the bred specimens made no difference to the arrangement and very little to the percentages (Table III).

Thus, in group 1, Zanzibar and Pemba have the smallest percentages, Tanganyika comes next and Uganda last with the largest percentages. The fourth type of wing is absent from Uganda and shows small percentages in the Islands and in Tanganyika.

The most striking figures are those for group 3. This group is poorly represented among Uganda specimens ; more common in Tanganyika, particularly in the coast towns Tanga and Dar-es-Salaam ; and forms by far the biggest proportion of Pemba and Zanzibar specimens. This seems to confirm the impression that the third group of wing characters represents a coastal form of *A. funestus*, particularly as the further one gets from the coast the rarer this type of wing becomes in the collections.

Pharyngeal armatures taken from each wing group proved to be identical and of the type form.

It is interesting to note that the two forms with the interrupted basal costal spot were absent from the Rhodesian material (Leeson, 1930 *b*) and that most of the specimens from that country had a dark preaccessory sector spot on the first vein opposite the proximal end of the second main dark costal spot. From South Africa DeMeillon (1933) reports two forms as having interrupted basal costal spots, which he says are quite common, though he does not give the geographical distribution.

Eggs.

292 females provisionally identified as *A. funestus* were put aside to deposit eggs. 160 batches of eggs were laid and all were found to be of the type form as described by Evans & Leeson (1935). Twenty-four pharyngeal armatures were dissected out and were found to support the identification. Some wings were damaged and could not be described with certainty, but 134 pairs were in sufficiently good condition to be accurately grouped. Once more there were the four types described above. There were 85 (64 per cent.) in group 1 ; 19 (14 per cent.) in group 2 ; 27 (20 per cent.) in group 3 ; and 3 (2 per cent.) in group 4.

Haunts of Adults.

In spite of intensive search throughout the whole tour no adult of *A. funestus* or its allies was found in outdoor haunts such as were described by Leeson (1931) as occurring in Southern Rhodesia.

TABLE IV.

Number of each species of A. funestus *series found in houses.*

A. funestus wing group 1	828 specimens
,, ,, ,, 2	243 ,,
,, ,, ,, 3	358 ,,
,, ,, ,, 4	42 ,,
	1,471 specimens
A. rivulorum	22 ,,
A. leesoni	0 ,,
A. rivulorum var. *garnhamellus*	8 ,,
Total	1,501 specimens

All adults were taken in native huts and gaols, European houses and other buildings. Native huts were sometimes occupied at night by cattle, goats and domestic fowls as well as by their owners: It can be said at once that by far the greatest number of mosquitoes frequenting these places were *A. funestus* and *A. gambiae.* Type form *A. funestus* is the chief species of the series as is shown in Table IV. This table shows the numbers of the specimens occurring in each wing group from a sample which was critically examined. Only 3 per cent. of these were males. The figures show that *A. rivulorum, leesoni* and var. *garnhamellus* rarely or never enter human habitations. Evans & Garnham (1936) have shown that the two forms of *A. rivulorum* occurring in Kenya rarely enter dwellings, and DeMeillon (1936) has similarly demonstrated that *A. leesoni* is also not a house-frequenter in South Africa.

Precipitin Tests.

The precipitin tests kindly done for me by Mr. C. B. Symes and his staff at Nairobi, Kenya, were done on the stomach contents of a large number of female Anophelines. Leaving out other species and a few " old bloods," there were 456 tests on *A. funestus.* Use was made once more of the pharyngeal armatures to confirm the identification: 239 (52 per cent.) showed positive reactions for human blood ; 6 (1 per cent.) positive ox blood ; 7 (2 per cent.) positive for both human and ox blood ; and 204 (45 per cent.) were negative for ox and human blood. Thus roughly half of the specimens contained human blood, very few ox blood and the remainder were negative for both. It may be that the latter results were due to the presence of blood other than those for which the tests were made.

Examination of the wings of these specimens showed that they all fell into the four groups already described. A random sample of 310 pairs of wings taken from the females submitted to the precipitin test was examined: 137 had wings of the first group, of which 69 showed a positive reaction from human blood, while 68 were negative for ox and human ; 80 specimens had wings of the second group and of these 43 showed a positive reaction for human blood and 37 were negative ; there were 73 in group 3, 32 positive human and 41 negative ; in group 4 there were 20 specimens, 6 positive human and 14 negative. Thus it would seem that no group is more addicted to feeding on human blood than another.

Infectivity.

Examinations of the stomachs and salivary glands of 122 female *A. funestus* were made for the presence of the parasites of malaria. Identifications of the females were checked by examination of the pharyngeal armatures ; all were of the type form. Two females (2 per cent. approx.) were found infected in both glands and stomachs ; 4 (3 per cent.) were infected in glands only ; 9 (7 per cent.) were infected in stomachs only ; and 107 (88 per cent.) were negative.

Upon examination of the wings of these females it was found that only the first three groups were present. This could be expected of course among so small a number, because, as already mentioned, the fourth group is much rarer than the others. There were 99 specimens in the first group and of these, 10 were infected ; 19 in the second group, of which 5 were infected, and only 4 in the third group, of which none was infected. It may be possible that if a sufficiently large number of dissections had been made that infected individuals would have been found in each of the four wing groups.

Geographical Distribution.

The distribution of the species is shown on the map (fig. 2) and in Table V. At Muko, Chabahinga, Soroti, Rhino Camp and Pakwach, all in Uganda, adults of *A. funestus* were very common in houses. In some places more than 150 specimens could be collected in three hours, yet larval collections showed only a few *A. funestus* at Chabahinga and none at the other places. *A. coustani* was the commonest larva at Muko and Chabahinga, mainly from Lake Bunyoni. *A. gambiae* larvae were common at Soroti from pits and similar depressions ; no typical *funestus* breeding-places were seen here. At Rhino Camp and Pakwach the commonest larva was *A. rivulorum* var. *garnhamellus*, taken from the River Nile among *Pistia stratiotes.*

These instances are excellent examples of the fact that the larval collections are not necessarily a guide to the species of mosquito infesting the houses. This has been recorded by several authors, including Ingram & De Meillon (1929) who noted that adults of *A. gambiae* and *A. funestus* were found in places in South Africa where, had reliance been placed on failure to find larvae, these mosquitoes would have been reported as absent. Earlier still, Johnson (1919) in Nigeria found that a totally false idea is obtained from a larval survey, as the common larvae may not be the common domestic mosquito.

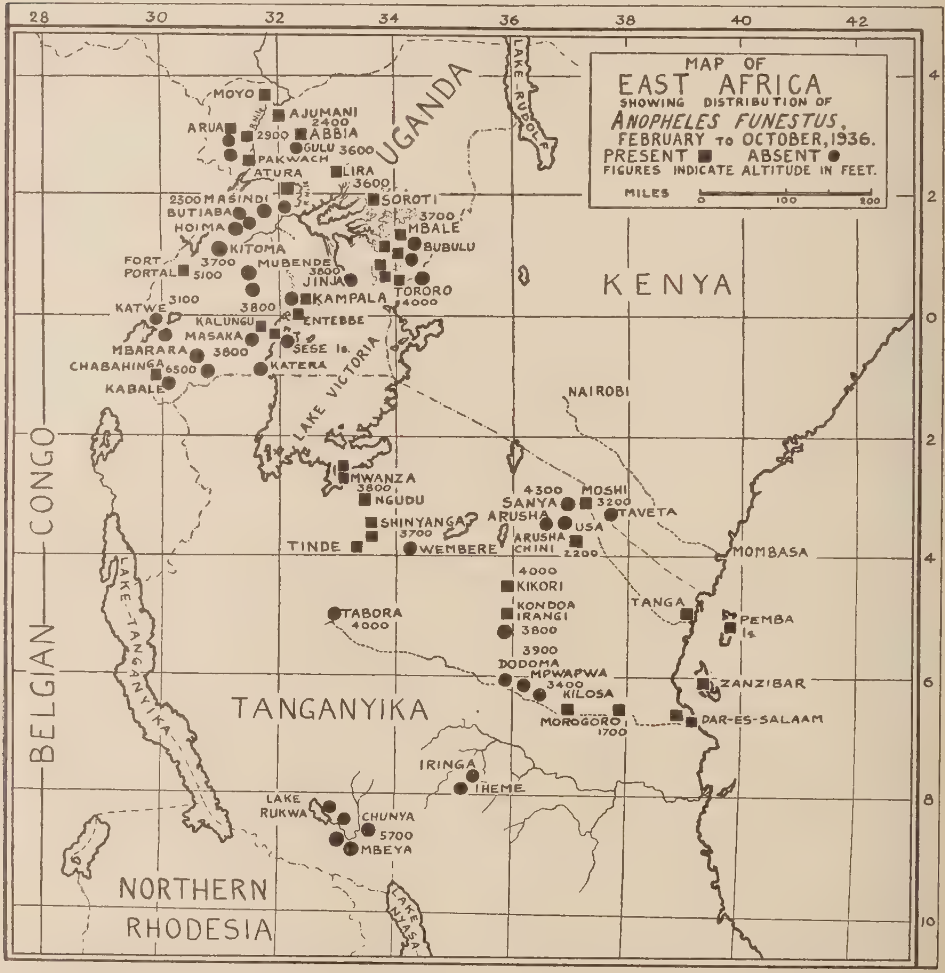

MAP OF
EAST AFRICA
SHOWING DISTRIBUTION OF
ANOPHELES FUNESTUS,
FEBRUARY TO OCTOBER, 1936.
PRESENT ■ ABSENT ●
FIGURES INDICATE ALTITUDE IN FEET.
MILES 0 100 200
28 30 32 34 36 38 40 42
4 2 0 2 4 6 8 10
UGANDA
KENYA
TANGANYIKA
BELGIAN CONGO
NORTHERN RHODESIA
LAKE RUDOLF
LAKE VICTORIA
LAKE TANGANYIKA
LAKE NYASA
LAKE RUKWA
NILE
MOYO
AJUMANI
2400
ARUA
2900
ABBIA
GULU 3600
PAKWACH
ATURA
LIRA
3600
2300 MASINDI
SOROTI
BUTIABA
HOIMA
3700
MBALE
BUBULU
KITOMA
FORT PORTAL 5100
3700
MUBENDE
3800
JINJA
TORORO
4000
3100
3800
KAMPALA
KATWE
KALUNGU
ENTEBBE
MASAKA
MBARARA
3800
SESE Is.
CHABAHINGA 6500
KATERA
KABALE
NAIROBI
MWANZA
3800
NGUDU
4300
MOSHI
SANYA
3200
TAVETA
SHINYANGA
3700
ARUSHA
USA
ARUSHA CHINI
2200
TINDE
WEMBERE
MOMBASA
4000
KIKORI
TANGA
KONDOA IRANGI
3800
PEMBA Is.
TABORA
4000
3900
DODOMA
MPWAPWA
3400
ZANZIBAR
KILOSA
MOROGORO
1700
DAR-ES-SALAAM
IRINGA
IHEME
CHUNYA
5700
MBEYA

Fig. 2. Map of East Africa showing location of places mentioned in the text.

TABLE V.

Distribution of A. funestus.

Month	Place	Altitude (feet)	Adults	Larvae
Uganda				
June	Muko	6,600	v. common	none
June	Chabahinga ...	6,500	v. common	few
June	F. Portal ...	5,100	few	none
June	F. Portal ...	5,000	few	none
February, March, May	Kampala ...	4,300	few	few
March, May	Tororo ...	4,000	few	few
February, March, May	Entebbe ...	3,800	few	few
March, May	Mbale	3,700	few-common	few
May	Lira	3,600	common	few
May	Soroti	3,600	common	none
April	Abbia	2,900	common	few
April	Ajumani ...	2,400	common	few
April	Rhino Camp ...	2,400	v. common	none
April	Pakwach ...	2,400	v. common	none
Tanganyika				
August	Kondoa ...	4,000	few	few
August	Kikori ...	4,000	few	few
July	Shinyanga ...	3,900	few	few
July	Mwanza ...	3,800	common	few
July	Tinde	3,700	v. common	few
July	Shinyanga ...	3,700	few	few
September	Arusha-chini ...	2,200	few	few
August	Kilosa	2,000	v. common	common
August	Morogoro ...	1,700	v. common	common
September	Dar-es-Salaam	—	v. common	common
September	Tanga	—	common	few
Zanzibar Protectorate				
September	Zanzibar ...	—	v. common	common
September	Pemba ...	—	v. common	common

Looking at the map again one notices strange gaps in the Uganda distribution and that in Tanganyika *A. funestus* was not recorded south of Dodoma as far as Mbeya and Lake Rukwa ; in fact, all members of the *funestus* series were absent from this part of Tanganyika. The places where *A. funestus* was not found are listed in Table VI. Altitude alone cannot be an explanation of the absence of the species, as it was found at similar altitudes elsewhere.

TABLE VI.

List of places where A. funestus *was not found.*

Month	Place	Altitude (feet)
Uganda		
June	Kabale	6 000
April	Mubende	5,000
May	Masaka	4,300
May	Jinja	3,800
June	Mbarara	3,800
April	Masindi	3,700
April	Kitoma	3,700
April	Hoima	3,700
April	Gulu	3,600
June	Mbarara	3,500
June	Katwe	3,200
April	Butiaba	2,300
Tanganyika—		
August	Mbeya	5,700
August	Chunya	4,700
September	Sanya	4,300
July	Tabora	4,000
July	Dodoma	3,900
August	Mpwapwa	3,000
August	Mpwapwa	2,800
August	L. Rukwa	2,800
August	R. Ruaha	2,500

In Uganda it is certain that so far as larvae are concerned some places were flushed out by heavy rain. In others, notably those in the neighbourhood of Mubende, Masaka, Masindi, Kitoma and Hoima, the commonest vegetation found in the water was papyrus, and very few larvae of *A. funestus* were ever found among these plants. In the southern parts of Tanganyika absence of rain caused rivers to dry up so that the country was extremely parched.

Breeding-places.

A. funestus larvae were taken in places similar to those previously described by the author (1931), De Meillon (1933) and others. Clear, shaded water in which is some growing vegetation appears to be essential. Such water is found at the edges of certain streams and rivers, and in some pools and swamps (Plate XV, figs. 1 & 2). Vegetation includes grasses and reeds of various kinds, and occasionally floating plants such as water-lilies, and more rarely the water lettuce (*Pistia stratiotes*). *A. funestus* was seldom found in the many papyrus swamps of Uganda but could be found among the fringing vegetation. In most places water in papyrus swamps contained red flocculent matter, but in Lake Bunyoni near Chabahinga papyrus was growing in quite clear water ; larvae of *A. funestus* were found here. Larvae were more often found among grass than among other forms of vegetation, and never in waters without vegetation. The situation of the larvae in the water was invariably close to the banks of streams or ponds, very seldom more than a few inches out into the current. Such places are where grass is most usually found.

Recording of Light at Breeding-places.

It is well known that *A. funestus* larvae occur in shaded situations, but no measurement of the degree of shade has yet been recorded. During this investigation an attempt was made to measure the amount of light at breeding-places. Two instruments were taken in order to get some information on this point. One was the Eder Hecht Grey Wedge photometer and the other a photo-electric cell and galvanometer.

The Eder Hecht instrument resembles a photographic printing frame. Light passes through a milk-white glass and again through another glass strip which is transparent at one end, but which gradually increases in opacity towards the other end, then through a clear calibrated strip of celluloid. A print of the scale is obtained on photographic paper when the instrument is exposed. After toning, fixing and drying the paper the last transmitted scale line is read and the figure compared with a table of relative light values.

The photometer should be used continuously in the same way as other meteorological instruments, as it is intended to record the aggregate light over a period. Best results, therefore, can only be obtained by the investigator staying a considerable time in one place. Consequently, the use of this instrument was abandoned at an early stage.

Mr. P. Ullyott, of the Department of Zoology, University of Cambridge, was consulted about a suitable photo-electric cell, and on his recommendation I obtained one and a unipivot galvanometer. I am greatly indebted to Mr. Ullyott for his advice and for calibrating the photometer for me. This instrument was wired so that it gave two sets of readings, one twenty times more sensitive than the other. The cell was always kept covered by a closely fitting, padded, opaque lid when not in use. On arriving at a collection of water the cell was exposed in the situation where the light was to be recorded. No additional shadows or reflected light from the operator or bystanders were allowed to fall on the cell. The number of milliamps registered was then recorded.

No regard was paid to whether any particular species or any larvae at all were to be expected. There was thus no selection whatever. All observations were recorded on the spot before moving on to the next place. Each reading was given a serial number and the corresponding collecting tube numbered accordingly. Other data included a description of the site and surroundings, state of sky, time of day, altitude and temperature of water. A " control " reading of the open sky was taken each time by holding the cell above the head at arm's length. Readings were always made between 10 a.m. and 3.30 p.m. and finally expressed as percentages of the " control " or available light.

Larvae of *A. funestus* occurred in 95 of the breeding-places where light readings were taken. All these places received less than 70 per cent. of the available light. Nearly two-thirds of them (61) received less than 30 per cent. and half of them less than 20 per cent. If the percentages of available light are grouped in tens (0–10 per cent., 11–20 per cent., and so on), it is found that the largest number of observations, namely 32, or one-third of the total, falls in the second group 11–20 per cent.

In the chart (fig. 3) these figures are plotted and those for *A. gambiae* are included for comparison. The preference of *A. funestus* for shady and of *A. gambiae* for sunny situations is well shown.

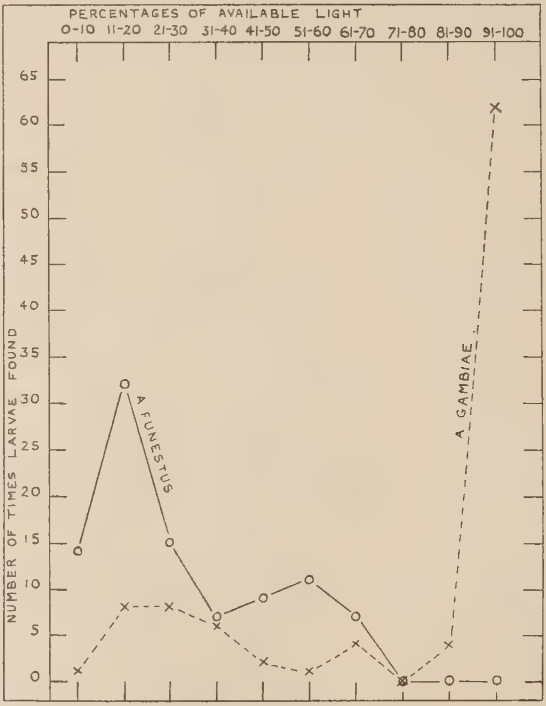


Fig. 3. Chart showing number of times larvae of *A. funestus* and *A. gambiae* were found in breeding-places of different light intensities.

In Table VII the numbers of observations in each group of light values are shown as percentages of the total observations recorded in that group. In waters having light values coming between 11 and 20 per cent., larvae of *A. funestus* were present in 21 per cent., *A. gambiae* larvae were only present in 5 per cent., while 24 per cent. of these waters had no larvae in them. In waters completely or nearly completely exposed to sunlight (91–100 per cent.) there were no larvae of *A. funestus*, but 42 per cent. of such waters contained larvae of *A. gambiae.*

The diagram (fig. 4) was constructed from the percentage figures given in Table VII. The total number of waters examined in each light group is shown as a column. The proportion of waters containing each species is represented by the shaded portions of the columns. *A. funestus* larvae are seen to be present in about one-sixth of the waters having light values up to 70 per cent. *A. gambiae* larvae occur in nearly half of the waters having little or no shade, while over one-third of all the waters contained no Anopheline larvae at all, whatever the condition of the light and shade.

TABLE VII.

Number of times larvae of certain East African Anophelines occurred in breeding-places of different light intensities shown as percentages of the total for each light group. Light figures are shown as percentages of available light and grouped in tens.

Species of larvae	Percentages of available light										Total numbers
	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	
	Percentages of each species occurring in each group										
A. funestus	18	21	15	10	13	17	15	—	—	—	95
A. gambiae	1	5	8	8	3	2	9	—	21	42	96
A. coustani	21	30	24	25	26	26	22	22	21	3	159
Other species	13	20	15	24	21	31	24	22	21	22	161
No larvae	47	24	38	33	37	24	30	56	37	33	254
	100	100	100	100	100	100	100	100	100	100	765

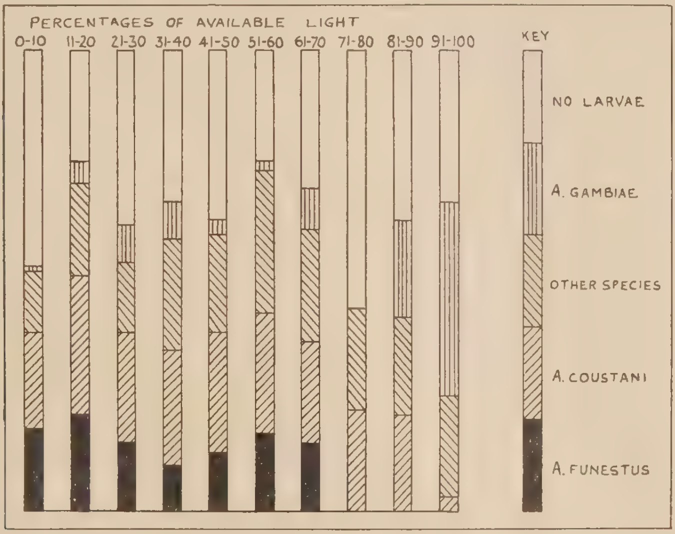


Fig. 4. Proportions of species of *Anopheles* larvae occurring in breeding-places of different light intensities. Light figures are shown as percentages of available light and grouped in tens.

A. rivulorum, Leeson.

This species was described by Leeson (1935) from material collected in Southern Rhodesia. Larvae and pupae from East Africa are quite typical, but two types of wing markings were noted among adults bred from previously identified and isolated larvae and pupae. The wing characters are shown in Table I. The presence of the dark preaccessory sector spot on the first vein opposite the proximal end of the second dark costal spot distinguishes this species at once from *A. funestus* as observed in East Africa. This character is new and is of considerable value in that it is not necessary to examine pharyngeal armatures to separate the species from *A. funestus*. This spot is, however, also present in the wing of *A. leesoni*, but *A. rivulorum* may be distinguished by the pale scaling on the third vein. In *A. rivulorum* the pale scales, when present, occupy a position mainly beyond the middle point, as in *A. funestus*, whereas in *A. leesoni* the pale scales, when present, are distributed equally about the middle of the vein.

There were two adults with wings of the first form and thirteen with wings of the second. They differ only in the markings on the upper branch of the fifth vein; the first has a pale area on this vein, while in the second this vein is all dark.

The bred material came from Abbia, Ajumani and Arua, in Uganda; no larvae of this species were found elsewhere. Adults caught in huts were taken at Abbia (4, 2 of each form) Lira (1), Soroti (1), Mbale (2), Entebbe (1), Chabahinga (2), and Muko (4), in Uganda; also at Kikori (1) and Moshi (2) in Tanganyika; all these were of the second form.

The type *A. rivulorum* from Southern Rhodesia has the third vein all dark. Adults with this form of wing were taken at Abbia (2), Rhino Camp (1) and Muko (1), all in Uganda.

Such small numbers among house collections indicate that *A. rivulorum* need not be regarded as an habitual house-frequenter. It also happens that no example of this species occurred among those dissected or among those upon which precipitin tests were performed or among those from which eggs were obtained.

The breeding-places of *A. rivulorum* were in a stream at Ajumani, the River Aswa at Abbia (Plate XV, fig. 2), and the River Ania at Arua, all in Uganda. Larvae were found among grass at the edges; there was no *Pistia* or other floating plant at these places. All were shaded by vegetation, but as larvae were so rare, light readings are very few, the highest being 70 per cent., as in the case of *A. funestus*. Two readings were below 10 per cent., two between 41 and 50 per cent., and two between 51 and 60 per cent.

Anopheles rivulorum var. **garnhamellus,** Evans & Leeson.

This variety has recently been described by Evans & Leeson (1937), and was recorded by Evans & Garnham (1936) as two forms of *A. rivulorum* from Kisumu and Digo, Kenya.

The larva has head-markings similar to those of *A. rivulorum* but the anterior dark transverse band has a tendency to be wider, so wide sometimes that it occupies nearly the whole of the anterior half of the clypeus. The main tergal plates on the abdomen are similar to those of *A. rivulorum*, but there is only one small posterior accessory plate on each segment instead of three. In the pupa, spine A is slightly shorter and the accessory paddle hair has fewer branches than in the type form.

Adults having two forms of wing were bred out (Table I). The wings differ from those of *A. funestus* in having a pale area on the upper branch of the fifth vein. In the second form there are two pale spots interrupting the dark basal costal area. From *A. rivulorum* and *A. leesoni* the variety differs not only in the interrupted basal costal area, but also in the absence of a dark preaccessory sector spot on the first vein; it is distinguished again from *A. leesoni* in the limits of the pale scaling on the third vein. One bred adult had wings of the first form and three had wings of the second. These came from Dar-es-Salaam; other larvae came from Atura, Abbia, Arua, Rhino Camp, and Pakwach, in Uganda; from Mwanza, Kilosa, Dar-es-Salaam and Arusha-chini, in Tanganyika; and from Zanzibar. Adults were caught at Abbia (1), Pakwach (1), and Dar-es-Salaam (1).

This mosquito is evidently of little importance, except for the adult's resemblance to *A. funestus*. It is not a house-frequenter apparently, and no examples were among those dissected or those upon which precipitin tests were made or among those which deposited eggs.

Evans & Garnham (1936), discussing the habits of the two forms of *A. rivulorum* in Kenya, found that the Kisumu form was not a house-frequenter, and the evidence regarding the Digo form, though not conclusive, tends to show that " *A. rivulorum* is not a house-frequenter in this region."

Larvae of *A. rivulorum* var. *garnhamellus* were taken in the Nile and other rivers, in pools, swamps and in an irrigation furrow. It was found among grass, elephant grass, but most frequently among *Pistia stratiotes* (Plate XVI, figs. 1, 2). Accurate light readings at breeding-places of this species were nearly always impossible to take because the larvae were so often found under the leaves of *Pistia*. At Jangwani, near Dar-es-Salaam, larvae were found in evil-smelling swamps of yellowish water having a salinity of 35 parts of chlorine to 100,000 water. In these waters no *Pistia* was present.

A. leesoni, Evans.

Larvae and pupae of this species were as described by Evans & Leeson (1935). Eight adults were bred from the collected larvae and pupae. All had one form of wing as shown in Table I.

The presence of the dark preaccessory sector spot on the first vein opposite the second main dark costal spot separates this species from *A. funestus* as seen in East Africa, and the extensive pale area on the third vein distinguishes the adults from those of *A. rivulorum*. But De Meillon (1933) records 5 females of *A. leesoni* out of 50 with the third vein all dark, 4 of them taken in May, a relatively dry month in South Africa. In addition, males of *A. leesoni* have three patches of pale scales on the club of the palps ; in other species only two are present, there being no such pale scales at the base of the palps.

Bred adults of this species were obtained only from Abbia in Uganda. Larvae were also taken at Ajumani and Arua, but no adults were caught anywhere either in houses or outside. De Meillon (1933 & 1936) records evidence to show that in South Africa *A. leesoni* does not frequent human habitations to any extent, though his numbers were very low.

Breeding-places were the Aswa River, Abbia (Plate XV, fig. 2) a stream at Ajumani and the River Ania, Arua. They were among grass at the edge and were in shade. Light readings are very few, but none is over 70 per cent.

Key to Adults of funestus *Series in Uganda, Tanganyika, Zanzibar and Pemba.*

1.—Dark preaccessory sector spot present ; base of costa uninterrupted............2
Dark preaccessory sector spot absent..3

2.—Third vein either all dark or with pale area situated mainly beyond midpoint ; ♂♂ with no pale scales at base of club of palp, that is, only two patches of pale scales..*rivulorum*
Third vein extensively pale ; ♂♂ with pale scales at base of club of palp, that is, with three patches of pale scales..*leesoni*

3.—Upper branch of fifth vein with a pale area ; base of costa interrupted by one or two pale patches.....................................*rivulorum* var. *garnhamellus*
Upper branch of fifth vein all dark ; base of costa uninterrupted or interrupted by one pale area only...*funestus*

Key to larvae of funestus *Series in Uganda, Tanganyika, Zanzibar and Pemba.*

1.—Anterior transverse dark band on clypeus..2
A pair of longitudinal dark stripes or areas on clypeus..........................*leesoni*

2.—Abdominal tergal plates large, deep, almost completely covering segments ; three small accessory plates on each main plate ....*funestus*
Abdominal tergal plates very shallow back to front...................................3

3.—Three small accessory plates behind each main abdominal tergal plate on segments V–VII at least...*rivulorum*

Only one small accessory plate behind each main abdominal tergal plate......... *rivulorum* var. *garnhamellus*

Summary.

The paper deals with *Anopheles funestus* and its allies as they occur in East Africa. The species dealt with are *A. funestus* type form, *A. rivulorum*, *A. rivulorum* var. *garnhamellus* and *A. leesoni*.

1. Differences between adults are so slight that they have until recently all been regarded as *A. funestus*. They may, however, be separated from one another by the points given in the Key (above). Differences between larvae of the species are much more pronounced.

2. It is also shown that, in this part of Africa at least, *A. funestus*, though reared from identical larvae and pupae, has four main forms of wing pattern. One of the forms of *A. funestus* appears to be absent from Uganda, while another form is much more prevalent in coastal regions than inland. *A. rivulorum* occurs in Uganda, but only two specimens were taken in Tanganyika. *A. rivulorum* var. *garnhamellus* is widely distributed throughout E. Africa. *A. leesoni* was found only in Uganda.

3. *A. funestus*, *A. rivulorum* and *A. leesoni* breed in similar situations, *i.e.*, clear, shaded water with growing vegetation. The larvae are more frequently found among grass than among other types of vegetation. Such breeding-places occur in rivers, streams, pools and swamps. Light readings taken at breeding-places corrobate the many reports that these larvae prefer shaded situations and are absent from exposed waters. Larvae of *A. rivulorum* var. *garnhamellus* are found most frequently associated with *Pistia stratiotes*, though on at least two occasions they were found in water where this plant was absent.

4. All the adults were taken inside buildings and none outside, in spite of continuous searching. Almost all were *A. funestus*, the remaining few were *A. rivulorum* and *A. rivulorum* var. *garnhamellus*; adults of *A. leesoni* were not taken at all. At several places, though adults of *A. funestus* were common in houses, very few or no larvae of this species were found; but larvae of the other forms were present. It is concluded that *A. funestus* is therefore an habitual house-frequenter and the others are not. Human blood was found in roughly half of the female *A. funestus* examined (239 out of 456); a very few contained ox blood and the remainder (204) were negative for ox and human blood. They were not tested for other bloods. Of 122 female *A. funestus* examined for malaria parasites 15 were found infected.

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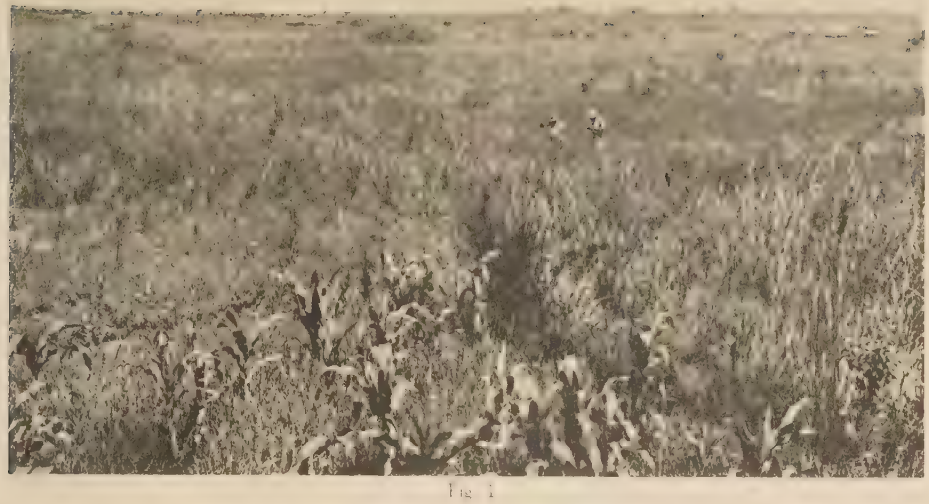

Fig. 1.

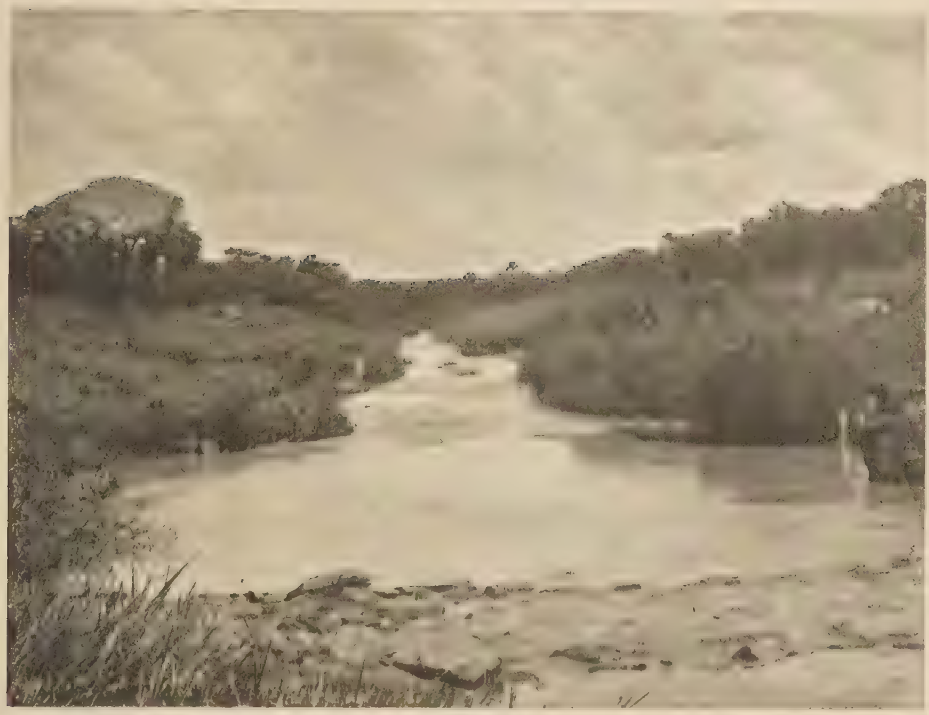

Fig. 2.

Fig. 1. Breeding places of *A. funestus*; swamp, Mbale, Uganda.

Fig. 2. Breeding places of *A. funestus*, *A. rivulorum* and *A. leesoni*; river Aswa, Abbia, Uganda.

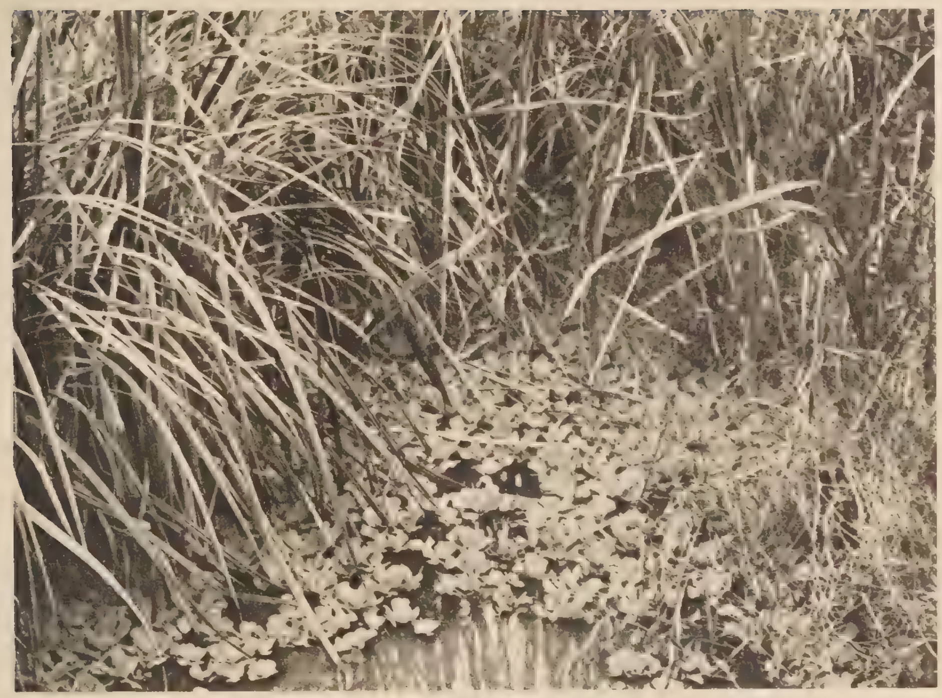

Fig. 1.

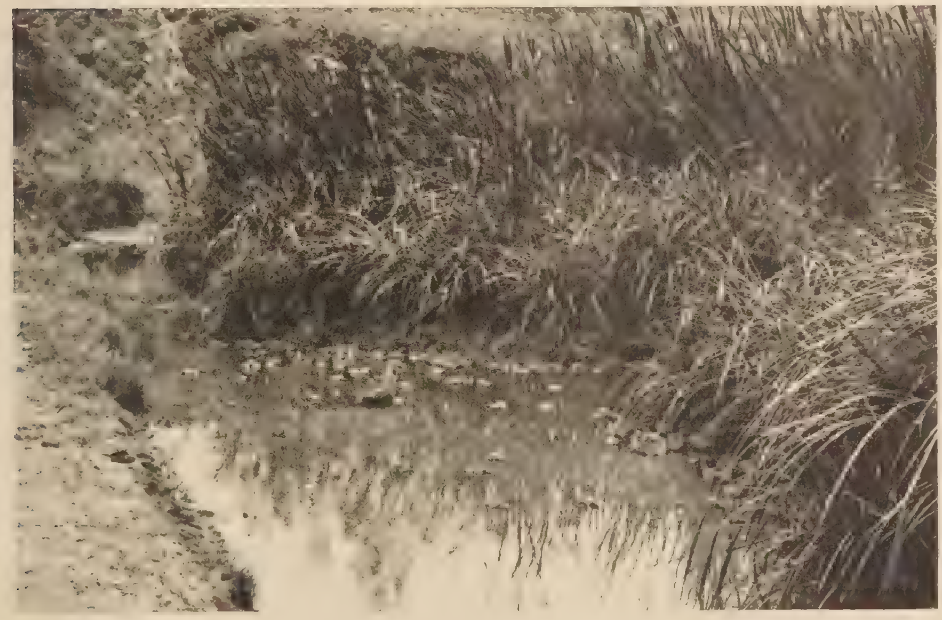

Fig. 2.

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Figs. 1 & 2. Breeding places of *A. rivulorum* var. *garnhamellus*.
Floating plants of *Pistia stratiotes*; Msimbazi, Dar-es-Salaam.

THE OUTBREAK AREAS OF THE DESERT LOCUST (*SCHISTOCERCA GREGARIA*, FORSK.) IN ARABIA.

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(Plate XVII & Map.)

As a result of several years work in the Anglo-Egyptian Sudan (Maxwell-Darling, 1934, 1936, 1936 *a*), it was concluded that the only outbreak centres of the Desert locust in north-eastern Africa were on the Red Sea coast. It appeared probable, however, that there existed other outbreak centres in Arabia, and unless those could be discovered and controlled, an outbreak originating in Arabia would spread into Africa and the Near East.

This paper presents the results of journeys undertaken on behalf of the Imperial Institute of Entomology for the purpose of locust investigations in southern Arabia. The Desert locust (*Schistocerca gregaria*, Forsk.) is the only species under consideration, as although solitary individuals of *Locusta migratoria*, L., occur in Arabia, this species has not been known to swarm there. The word locust means, in this paper, *Schistocerca gregaria* unless otherwise stated.

It must be understood that the time at the author's disposal for the survey of large areas was limited, and that only rough conclusions could be arrived at in most cases. In addition, it was not possible, in certain localities, to make more than a brief inspection, owing to the attitude of the inhabitants, who tend to regard locust investigations as a cloak for more sinister activities.

Types of Country.

The Arabian peninsula, of which rather less than half lies within the tropics, may be roughly divided into mountains, steppe and sandy areas.

Ranges of hills run along the coast almost continuously from the Gulf of Aqaba down the Red Sea coast, along the south coast and up to Ruus el Jubal in Oman. These attain their greatest height and breadth in the south-west (Asir and Yemen) and in the Jebel Akhdar range in Oman.

A large part of the interior of northern and central Arabia consists of steppe country, with mostly hard ground and gravel. The largest sandy areas are the Ruba' el Khali in the south which joins up by narrower tongues of sand with the Nefud in the north. The Red Sea coast, the Trucial coast and parts of the south coast are also sandy. Although Arabia is often regarded as being " desert," there is probably no part of the peninsula with as little vegetation as parts of the Libyan desert.

Climate.

Meteorological stations, except on the Iranian Gulf, are few and far between, so that most information about rainfall is based on the statements of travellers and the Arabs.

The rainy season is not so definite as in many arid countries, but the larger part of the peninsula gets most of its rain in the winter and spring (November–April). The high mountains in the south-west and south-east and the country lying between them receive monsoon rains and some winter rain as well.

To the north of the Ruba' el Khali, the rainfall is usually heavier towards Iraq and Syria than in the central regions such as Nejd. In the latter areas, most of the country is suitable only for nomads, and rain-cultivation is not practised. Such cultivation as exists is dependent on floods or irrigation from wells or springs.

The high mountains of the south-west and south-east receive a heavier rainfall (perhaps 300–400 mm. in the year), so that rain-cultivation is possible. These are the most fertile parts of Arabia.

The southern half of the Red Sea coast has, in a good year, sufficient rainfall and floods from the mountains for cultivation to be carried out on a large scale, both in the wide deltas of wadys, and also on the sandy coastal plain.

The southern coast near Aden has a low rainfall, but flood-cultivation goes on in the beds of wadys which flow from the hills. Eastwards of Aden, the conditions are less favourable, as the Hadramaut mountains get less rain than those of the Yemen.

The only other areas which contain much cultivation are Dhofar on the south coast, the Batina coast north of Muscat, and the Hasa oasis. In these places, the crops depend on irrigation.

As regards temperatures, the northern inland parts have a hotter summer and a colder winter, while in the southern parts more stable conditions obtain. The coastal regions are, of course, much damper and experience a smaller range of temperature.

Scope of Investigations.

There is probably no part of Arabia, which is not visited by locusts during their swarming cycle, and most of the peninsula is very suitable for breeding, if the rains are sufficient. Information of locust movements in Arabia are naturally very scanty, but it is probable that, during the years in which swarms are in existence, they continue their activities in the centre and south for some time after they have disappeared from the northern parts (Iraq, Palestine and Syria).

In the time at the author's disposal it was not possible to survey the whole of Arabia, however briefly. It was decided, therefore, to confine the investigations to the parts which seemed most likely to contain outbreak centres.

It is known that areas which support a permanent solitary population of *Schistocerca gregaria* in any numbers are sandy regions with perennial grasses and undershrubs. Secondly, the outbreak centres on the Red Sea coast exhibit certain definite features, which may be summarised as follows :—

1. A very variable rainy season which, in a good year, may last for four months and total 250 mm. in the season.

2. A warm climate in the winter, which is the rainy season.

3. The presence of restricted areas in which the solitary locusts remain and become crowded instead of being thinly distributed over the whole region. These concentrating areas are, in the case of the Red Sea coast, patches of rain-cultivation on sand.

These facts made it possible to narrow down the investigations in Arabia to some regions which might be suspected of containing outbreak centres.

The northern parts of the peninsula were ignored, as it was considered that the climate during most of the rainy season would be too cold to favour the rapid breeding of solitary locusts.

The mountains and the steppe regions of central Arabia were also considered unimportant owing to unsuitable soil conditions. It was decided, therefore, to investigate the sandy regions of the centre and south. They can be roughly classified, in order of their relative extent, as follows :—

1. The Ruba' el Khali and its borders.
2. The Dahna near the Iranian Gulf, and the strips of sandy country in Nejd.
3. The Oman coasts.
4. Parts of the south coast.
5. The southern half of the Red Sea coast.

The rest of this paper gives an account of observations in some of these localities.

The Red Sea Coast.

The southern part of the Red Sea coast of Saudi Arabia was toured by car in March 1936. This area stretches from Jidda in the north to Jizan in the south.

The coastal plain near Jidda is about 5 miles wide, and consists of rather hard, coarse sand. There are salt pans near the sea, and loose dunes, covered with *Panicum* and *Lasiurus* tussocks, near the hills and in valleys among them. There were exceptionally good rains during the winter of 1935–36, so that the vegetation was thicker than usual. This vegetation was of the same type as the hard open plain and *Panicum* dunes at Khor Ashat, on the Sudan coast (Maxwell-Darling, 1936). There was a fair amount of rain-cultivation (*Pennisetum* millet and water melon) near Jidda in March, but this was apparently unusual and most of the ground did not look as if it had been cultivated regularly.

Odd solitary *Schistocerca* adults could be found all over the plain and more commonly (2–10 per hour) in the cultivation. In an outbreak centre on the Red Sea coast, one would expect to find abundant solitary adults in March and bands of hoppers in early April, after a good rainy season. The above numbers are, of course, far too small to be of any importance.

Southwards of Jidda the plain opens out and, except at Khor el Birk where the hills come down to the sea, remains wide as far as Jizan and beyond. It is about 25 miles wide at Jizan.

It was not possible to go all over the plain in the cars available, as there is a great deal of soft sand in places. The road goes near the sea for the most part. From Jidda to near El Lith the country is mostly undulating sand covered with tussocks and annuals, and with a fairly firm surface owing to the rains. There were only a few patches of cultivation, and very little *Suaeda*. Solitary *Schistocerca* adults and hoppers were to be found in small numbers all along the route, but particularly on dunes near the beginning of the salt pans which border the sea.

At El Lith is the first big wady. There are large patches of light clay in the delta which is cultivated, and much drifted sand. Solitary locusts were much more numerous here, both hoppers and adults. Here also, we begin to find more *Suaeda* bush.

Southwards of El Lith is the country called Asir. The mountains of Asir are much higher than those farther north, and normally receive a heavier rainfall. The coast of Asir also receives more rain normally than the Hejaz coast. There are many large wadys flowing from the hills across the coastal plain into the sea. Most of these expand into deltas, which are in some cases 4 or 5 miles wide. The soil in these deltas is mostly a light clay with sand at the edges. The whole country had received good rains in the year under consideration, and cultivation was abundant. The wadys had flooded a great deal in the winter, and several of them flooded again in early April. Rainfall had also been considerable, so that there was plentiful cultivation (mostly *Pennisetum*) on sand outside the wadys. In fact from El Lith to Jizan there was cultivation in view most of the way, except near Khor el Birk where the country is stony. These wadys are fertile for some way inland, and the country is settled, with villages and a few towns.

Schistocerca adults were abundant in all this country, particularly in the sandier parts of the cultivation. The majority were of the first winter generation and sexually mature. Young hoppers were not very abundant, but the conditions made an outbreak appear quite probable.

The similarity of this country to the African shore of the Red Sea was sufficient to justify its being regarded as an outbreak area. This conclusion was confirmed when a marching band of *congregans* hoppers was discovered near Sabia. So far as could be ascertained there had been no flying swarms in the country during the season.

These conditions probably extend down the coast of the Yemen. The author was unable to visit the latter, owing to political difficulties, but Mohammed Effendi Hussein, Entomologist of the Egyptian Ministry of Agriculture, has been carrying on investigations there during the past winter (1936–37).

Numerous solitary *Locusta migratoria*, L., adults and some swarm-coloured hoppers, were found in a dense growth of a Cyperaceous plant on clay ground south of the Khor el Birk. Incipient swarming of this locust has often been observed on the African Red Sea coast, but the swarms have never migrated.

The Western Part of the Southern Coast.

The coastal plain near Aden is about 25 miles wide, but becomes narrower near the Bab el Mandeb straits to the west, where it also becomes stony.

This part of the coast was visited four times, through the kindness of the Sultan of Laheg, *viz.* in October 1935, February 1936, May 1936 and August 1936.

The wide part of the plain consists of a hard clay, sand and gravel floor, which is more or less covered with sand. The country is gently undulating near the sea, but the northern half of the plain near the hills consists of high sand hills. The sand is loose but by no means bare. There is a vegetation of undershrubs and tussock grasses of the density usually found on sand, the commonest plants being *Panicum turgidum*, L., *Odyssea mucronata*, Stapf, *Periploca* sp., *Heliotropium undulatum*, Vahl., *Dipterygium glaucum*, Decne. Annuals are few and are never dense enough to cover the ground ; the commonest are *Indigofera hochstetteri*, Bak., *Tribulus mollis*, Ehrenb., and *T. pterocarpus*, Ehrenb. The upper portions of high dunes are bare. There are practically no trees or bushes, except in the beds of wadys or where there is ground water. Near the sea, where the ground is flatter, *Panicum* is the commonest perennial. There are a few areas only in which *Suaeda fructicosa*, Forsk., occurs.

There are a number of wadys running from the mountains across the plain into the sea. Wady Bana', Wady Ahwar and Wady Tiban (in which Laheg is situated) are the largest of these, and the latter might be termed a river, as a little water flows in it all the year round. Owing to the scarcity of rain on the coast, cultivation is confined there to the wadys, and depends on flood water from the mountains. Considerable ingenuity is shown in damming and distributing this water. The larger wadys begin to expand into deltas shortly after leaving the hills, and there are large areas of good clay and silt. The smaller wadys have usually small deltas near the sea, but the Arabs have a system of holding up soil and forming plots in the upper reaches which would otherwise consist of stony and sandy wady-beds.

Nearly all the trees on the coast are found in the beds or deltas of wadys. These include *Acacia* spp., *Zizyphus* sp., *Salvadora persica*, L., and tamarisk. The only bushes which occur outside the wadys near the sea are *Calligonum comosum*, L'Herit., and *Suaeda fructicosa* in places. The cultivation consists mainly of dates, dhura (*Sorghum* millet), sesame, a little cotton and dukhn (*Pennisetum* millet).

Climate of the Aden Coast.

The only figures available are for Aden peninsula itself. The following table shows the mean monthly rainfall and maximum and minimum temperatures calculated over a period of 18–50 years. These figures were obtained from the Meteorological Office, London.

TABLE I.

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Maximum °C.	26·7	27·2	28·9	31·1	33·9	35·0	33·9	33·3	33·9	32·2	29·4	27·2	—
Minimum °C.	22·8	22·8	23·9	25·6	27·8	28·9	28·3	27·2	28·3	25·6	23·9	22·8	—
Rainfall mms.	8·6	4·6	10·7	6·1	3·8	1·3	0·8	2·8	3·1	3·1	1·8	3·3	49·8

The above temperatures show a stable climate, with small differences between winter and summer, and a very small daily range of temperature. Aden peninsula is very damp ; even a few miles inland the atmosphere is appreciably drier with the result of a higher maximum and lower minimum temperature. The rainfall figures indicate a very low rainfall with no well defined rainy season, although January to April are the rainiest months. It is probable that near the hills there is heavier rain in the monsoon, as there is more vegetation in that area. The Arabs distinguish between summer (March–May) and monsoon (August–September) rains ; and they say that less rain falls in the winter.

Locusts on the Aden Coast.

In September 1935 there was a little breeding of *gregaria* swarms at El Raha and Um Shaebi, east and west of Laheg respectively. The resultant young swarms flew north during the first half of October. Stragglers from these swarms caused a certain amount of confusion with the solitary population during the author's first visit to this part of the coast. Subsequent visits corrected some false impressions.

This country was seen during two breeding seasons—October 1935 (the end of the monsoon) and May 1936—when there was summer rain in one area. The population of solitary locusts was smaller than had been observed during any breeding season on the Red Sea coast of the Sudan. There were few locusts on the open plain and dunes, and the majority were found in and near the wady beds. The big wadys contain a large amount of clay, and very few locusts can be found except at the edges or in other parts where the soil is sandier or lighter in texture.

The largest populations of solitary locusts were seen in the following places :—

1. Wady Um Rija, west of Laheg. This was at the end of May 1936, and good rains (perhaps 50–70 mm.) had fallen at the beginning of May over an area of a few square miles. The country outside the wady was green and there were half-grown crops in the wady beds. The area between the edge of the cultivation and the dunes at the edge of the wady contained about 20 locusts per man-mile. These were all sexually mature. When this area was revisited in August 1936, very few locusts were to be seen. If early monsoon rains had come at the end of July, one would have expected a second generation of these locusts, and a large increase in numbers. But in the year in question there was no rain at this time.

2. In Wady Bana', east of Aden. The delta of this wady, known as Abyan, contained a much higher population of locusts than the Laheg delta in Wady Tiban, in December 1935. The soil was moist from floods two inches from the surface, and the locusts were sexually mature, although the only rain since September had been a little drizzle. In June 1936, most of this area was dry and there were very few locusts. There had been no summer rain.

3. In Wady Ahwar, east of Wady Bana'. This wady was visited only once, in June 1936. Locusts were to be found all over the edges of the cultivation, and a higher population was present in an area of 5–10 acres, where the soil was sandy and moist near the surface. These locusts were sexually mature, although there had been hardly any summer rain.

These instances show that breeding can take place with very little rain, where moist soil and green vegetation occur. Doubtless, microclimatic conditions account for this. It is probable that breeding would occur on a larger scale when heavy rains fell.

The Coast of the Hadramaut.

Wady Hadramaut is an inland valley, but the term Hadramaut is commonly used to designate a large area of country, and it is used here in that sense.

The author visited Mukalla and the country between Mukalla and Shehr to the east. This strip of coast is largely rocky. There are small areas of dunes of about one mile in breadth, and cultivation depends on irrigation from wells or springs. In the only large piece of cultivation (tobacco) at Ghel Ba Wazir, no *Schistocerca* were found, although *Locusta* and other ACRIDIDAE were common. Rainfall would appear to be less than farther west, judging by the vegetation.

The coast between Mukalla and Ahwar has not been visited, nor has that to the east of Shehr.

Summary of the South Coast.

It will be seen from the above that conditions on the southern coast of Arabia are less favourable for the production of phase *congregans* than those obtaining on the Red Sea littoral. The areas of rain cultivation on sand are lacking, but there are definitely certain areas in which locusts would become crowded if they multiplied sufficiently.

On the whole, we must regard the coastal plain between the Bab el Mandeb straits and Ahwar as a possible outbreak area of *Schistocerca*.

There may be other suspicious places between Ahwar and Mukalla. The coast eastwards of Mukalla to Ras el Had is said to be very barren, with the exception of Dhufar. But there are large sandy plains in some parts of this stretch, and it should be investigated. Unfortunately, this is one of the most difficult parts of Arabia to visit.

The South-western Borders of the Ruba' el Khali.

The term Ruba' el Khali is here used to mean the whole of the great inland desert of southern Arabia. In order to reach its southern edge, the mountains which separate it from the coast have to be crossed.

Soon after entering the foothills the soft sand of the coastal plain is left behind. Routes usually lie up the beds of wadys flowing seawards, among the hills. There are plains of light clay, such as El Kor in the Audali country and the plain near Jaza in the Aulaqi country. These mountain regions receive more rainfall than the coast, and there are large areas of rain cultivation. Solitary locusts are rare, but not absent. The uncultivated parts of the plains are covered in places with dense woods of *Acacia* spp.

These remarks apply to the western mountains. The high limestone plateau of the Hadramaut is more barren, and cultivation is confined to wadys.

After the watershed has been passed, there are wadys flowing into the Ruba' el Khali which are sandy in their lower reaches. Some of these wadys are inhabitated and cultivated. We shall consider Wady Beihan.

Wady Beihan rises in the mountains and flows into the desert on the border of Aden Protectorate and the Yemen. It is permanently inhabited and has many castles and a few large villages. The tribes in the lower reaches are semi-nomadic, as they live in the desert at times.

The wady becomes sandy for about the last 20 miles before it leaves the mountains. In this stretch it is 1–2 miles wide but opens out as it reaches the end of the hills. This is the stretch under consideration. The wady bed is sandy and stony for most of its length and about 200 yards wide. On either side of it are clay banks, artificially constructed. If there is a series of years without any flood, this land becomes more sandy. Outside these clay banks are loose sand-dunes, with *Salvadora persica*, *Dipterygium glaucum*, *Rhazya stricta*, and *Tephrosia* sp. among them. Near the hills there are more, but sandier, banks which are flooded from the hills if there is any local rain.

The main cultivation depends on floods from the hills at the source of the wady, where there is more rain than in the lower reaches. But there is also a certain amount of irrigation from wells. In spite of the anarchic conditions prevailing in the wady, there are regulations governing the water supply, so that one man may not take too much. These regulations are apparently observed. Each piece of land is watered from a channel brought from upstream, where a bank is built to direct some of the flood water into the channel. When the water has reached a certain depth in a given field, it is the duty of the owner to open the bank at the lower end of his field in order that the water can flow on to the next. In spite of this arrangement, only a very big flood will reach the lower cultivation near the desert. The latter part of the wady contains more cultivable land than the upper reaches, but the soil is sandier, as it gets flooded more rarely.

As the desert is reached, *Salvadora persica* is largely replaced by *Calligonum comosum*, and the former is not found in the desert itself. The desert was inspected as far as El Milh, a salt mine about 30 miles from the edge of the hills. The desert consists of loose sand-dunes for the most part, but there are wide corridors of flat coarser sand among them. The only bush or tree seen in this area was *Calligonum comosum*, which was very scattered, and there were large areas with none. The ground was for the most part completely bare, but there were patches of annuals in places where there had been rain four months before (*i.e.*, in September 1935). These consisted of *Achyranthes aspera*, *Cerastium* sp., *Tribulus* sp., *Cyperus* sp. and *Neurada procumbens*. *Panicum* was noticeably scarce. This vegetation resembled in appearance the *gizzu* vegetation of the north-western Sudan (Maxwell Darling, 1934 and 1936 *a*).

Wady Beihan is recognisable out in the desert only by the greater amount of vegetation in its course, as its bed is mostly blocked with sand. There are, however, occasional patches of flood clay observable. The cultivation consists of *Zizyphus* trees, which are pollarded and the leaves and twigs used as fodder, *Indigofera* sp. from which indigo is made, sesame, a little cotton, and wheat and barley in the winter and *Sorghum* in the summer. *Zizyphus*, *Indigofera* and cotton are perennial and to some extent independent of surface water.

Climate.

Wady Beihan lies at an altitude of over 4,000 ft., so that very high temperatures do not obtain. The temperature is higher in the summer than might be expected, as a north wind blows frequently from the desert. The temperatures observed by the author were in January, max. 28·7°, min. 12·4°C., relative humidity 31–66 per cent. ; in July, max. 37·4°, min. 24·5°C., relative humidity 6–39 per cent.

The rainy seasons, according to the Arabs, are spring (March–April) and monsoon (July–September). Rain may come in both seasons or in neither. The author spent six weeks in Wady Beihan in 1936, a fortnight in February, and a month in July.

A small quantity of rain fell in February (perhaps 1 mm.) and more in March, when a small spate of water came down the wady. During July and the first week of August, there were frequent thunderstorms and rain in the mountains, but only drops or light showers fell in the lower part of the wady ; this rain was not sufficient to affect the vegetation. There was a very small flood in July, and a slightly larger one at the beginning of August. In neither case did water reach the end of the cultivation.

The only way of estimating the annual rainfall is by the amount of perennial vegetation. The country outside the flooded area of Wady Beihan consists of bare dunes with hardly any perennials. Such dunes can exist in places with an annual rainfall of about 200 mm., when they are due to exceptionally strong winds as near Tokar, or to cultivation as at Khor Ashat. These two places are on the Red Sea coast of the Sudan.

Near Beihan, where neither of these factors operates, loose bare dunes must be attributed to a very low rainfall, smaller than that of the Aden coast, and much smaller than that of the Red Sea coast.

Locusts in Wady Beihan.

The population of solitary locusts in Wady Beihan is very low. Only 12 specimens were found in six weeks. These were all in sandy places where there were some perennials, outside the main cultivation. Some breeding took place during the rains in March, as a few freshly moulted adults were present at the beginning of July. No locusts were found in the desert outside the hills.

Conclusions on the Beihan Area.

It appears unlikely that rainfall is ever sufficient in the sandy areas of the wady for the breeding of solitary locusts to occur on a large scale. Higher up the wady, where rainfall is heavier, stony and clay soils exist, which form an unsuitable habitat. The low rainfall, coupled with the low locust population, enable us to say that it is very improbable that this area is an outbreak centre.

These conditions also prevail in Wady Hadramaut and the Wadys at Nisab, and doubtless along the whole south-west border of the Ruba' el Khali.

Wady Hadramaut contains more irrigated cultivation, partly owing to the presence of an artificially high population, living on money from abroad. But apart from this, the rainfall and soil conditions are similar to those of Beihan. Wady Hadramaut is farther from the northern edge of the mountains than is Wady Beihan, and unlike the latter, it does not flow into the desert, but into the sea.

Oman.

Oman is the south-eastern corner of Arabia, and is bounded by the sea to the north, east and south, and by the Ruba' el Khali desert to the west.

The range of mountains comes right down to the sea between Muscat and Ras el Had. North of Muscat there is a coastal plain, the Batina, which is about 10 miles wide at its greatest breadth. The coast at the northern peak, Ruus el Jubal is again mountainous, but the mountains recede far inland westwards along the Trucial Coast. To the south-west beyond Ras el Had, there is a coastal plain. This latter area and the desert inland of it were not visited by the author.

Climate.

Muscat is just north of the tropic of Cancer, so that the northern part of Oman experiences a colder winter than does Aden or the southern part of the Red Sea coast. The mountains in the interior of Oman, and the coast south of Sur have some monsoon rains, but on the northern coasts the rainy season is the winter (November–March).

The following figures (Table II) for Muscat were obtained from the Meteorological Office, London.

TABLE II.
Muscat (18–38 years).

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Maximum °C.	23·9	24·4	27·2	31·7	35·6	36·7	35·0	32·8	32·8	32·8	28·9	25·6	—
Minimum °C.	18·9	19·4	22·2	26·1	29·4	31·1	30·6	28·9	28·3	26·7	23·3	20·6	—
Rainfall mms.	28	18	11	9	0	2	1	1	0	3	10	17	100

The following table gives the monthly averages for Sharja on the Trucial Coast of Oman for the three years 1934, 1935 and 1936.

TABLE III.
Sharja (3 years).

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Maximum °C.	22·9	24·4	26·4	29·6	33·8	35·8	37·8	39·0	36·7	33·3	29·9	25·6	—
Minimum °C.	11·3	13·2	14·6	18·4	22·3	25·2	27·1	27·7	25·1	21·3	17·3	15·4	—
Rainfall mms.	20	35	17	2	0	0	0	0	0	0	38	37	149

The three-year averages give, of course, only a very rough idea of the climate, but the figures indicate that the Trucial Coast has a colder winter than Muscat, higher maximum and lower minimum temperatures in the summer, and a higher rainfall. The greater daily range of summer temperatures at Sharja is probably due to the open nature of the country, whereas Muscat is shut in by mountains.

The Coast South of Muscat.

The coast from Muscat to Ras el Had is nearly all rocky, but there are occasional sandy bays where the hills recede. One such locality, Qeriyat, was visited in January 1937. Here there is a sandy plain about four miles long and three miles broad at its widest point. There is a small wady coming down from the hills and a fair amount of cultivation irrigated from wells. This consists of dates, wheat, barley, dukhn, vegetables and lucerne and fruit trees.

At the southern part of this plain is an area of sand-dunes, apparently formed of sea-sand. On their lower levels there is a vegetation of *Heliotropium undulatum* and *Prosopis spicigera*, a tree. The higher dunes had no vegetation except a sparse *Cyperus* and a few *Leptadenia* bushes. There had been no rain at the time, and no locusts were found.

There is a similar area to the above at Sur, near Ras el Had.

The Batina Plain.

The Batina plain is about 180 miles long and about 10 miles in width at its widest point. It may be divided into the following zones parallel with the sea.

1. The sandy beach with some dunes, on which the villages are situated.
2. The cultivation, which is almost continuous right along the plain, and is $\frac{1}{4}$–1 mile wide.
3. The narrow tree belt.

4. The open plain.

1. The villages, which form an almost continuous row up the coast, are mostly situated on a narrow belt of sand-dunes near the beach. Hardly any vegetation grows on these dunes, except in a few places where there are no villages.

2. The cultivation is mostly on clay soil, some of which is salty. Dates form the bulk of the crops, but grains, fruit and vegetables and lucerne are also grown. The land is irrigated from wells and occasionally from springs, and in a few cases flood water is diverted from wadys.

3. The belt of trees adjoining the cultivation may be as much as ½ mile in width. The trees are as dense as an orchard in places, and consist mainly of *Prosopis spicigera* and *Acacia tortilis*. The ground here is mostly hard sand and clay, bearing a vegetation consisting largely of the annual *Asphodelus tenuifolius*.

4. The open plain is formed of hard sand and clay with a little gravel. This type of ground is called in Oman *sih*. Nearer the hills it becomes more stony. There are hardly any trees. The commonest undershrub is *Tephrosia nubica*, and *Salicornia fructicosa* and *Asphodelus tenuifolius* are abundant. There are a few small sandy runnels with a denser growth of *Tephrosia nubica*.

There are a number of wadys flowing across the plain. Many of these flow into the sea without spreading out. Some spread out into the cultivation. The bed of these wadys is usually sandy, and may contain islands with some vegetation. The wider wadys also have sand-dunes on their banks, and sand stretching for a few hundred yards on each side. In some cases these dunes have *Salvadora* bushes on them, and *Heliotropium undulatum*. The sandy ground has a vegetation consisting mostly of the annuals, *Trigonella hamosa*, *Cenchrus ciliaris*, and two small procumbent Leguminosae. This sandy ground spreads into the cultivation in places.

Solitary locusts in the Batina.

Rains had been fairly good over most of the Batina during the winter 1936–37, and about 15 mm. fell during the author's visit in February.

Searches were made in many localities, but particularly in the sandy places. The only area in which any locusts were found was near Sohar, in a sandy area near the wady, as described above, and away from the cultivation. On the dunes by the bank of the wady, and on the sandy ground among the trees near by, about 20 hoppers were found in one hour by two men. These were green 4th and 5th instar hoppers, and were presumably of the first winter generation. The absence of locusts in the other sandy areas which were inspected was surprising.

The Trucial Coast and Interior.

This area was toured during the latter half of February and March 1937. Rains had been exceptionally heavy during the season, and about 230 mm. were recorded at Sharja from November 1936 to March 1937. There was probably more rain than this in the interior.

The parts visited by the author were the coast from Ras el Kheima, near the Ruus el Jubal cape, to Abu Dhabi in the west ; about 10 miles inland from Dubei ; from Abu Dhabi to Bareimi at the edge of the hills in the interior, about 70 miles westwards from Bareimi and back to Abu Dhabi.

The mountain range of Oman reaches its northern point in the Ruus el Jubal cape. West of this point the hills recede southwards, so that nearly all the Trucial Coast is an open plain with no hills visible. This plain is almost entirely sandy. There are no wadys flowing into the sea west of Ras el Kheima, as the local rainfall is absorbed into the sand, and any water flowing from the distant hills does not reach the coast.

The coast near the sea consists of white sand with the following plants growing on the dunes : *Lithospermum callosum*, *Medicago aschersoniana* and *Cyperus arenarius*.

In March 1937 these plants were green and fairly abundant, although there was always bare sand among the plants. The dunes had been rendered firm by the heavy rain. There are usually salt-pans near the sea, which sometimes stretch for some miles inland.

About 10 miles inland the sand becomes redder in colour, and the dunes are higher. From Abu Dhabi to Bareimi, the general aspect of the country is high dunes enclosing valleys about two miles long and one mile broad. The high dunes themselves bear very little vegetation. The sandy valleys resemble the north-central African gozes (Maxwell-Darling, 1934 and 1936 *a*) in the amount of vegetation they bear, but unlike the gozes, their sand is soft. The following perennial undershrubs and grasses are common : Grasses : *Panicum turgidum*, *Pennisetum dichotum*, *Cyperus cruentus*, *Aristida plumosa* ; undershrubs : *Lithospermum callosum*, *Heliotropium undulatum*, *Salicornia fructicosa* ; and the following herbs : *Malcolmia aegyptiaca*, *Launaea mucronata*, *Tribulus lanuginosus*, *Medicago aschersoniana*, *Cyperus arenarius*.

The lowest-lying portion of the valleys among the dunes will often consist of hard *sih* which is sometimes partly a salt-pan. In such places the vegetation consists mostly of the succulents, *Zygophyllum album* and *Zygophyllum* sp., and the herb *Arnebia hispidissima*.

There are very few trees in the Oman sands, but there are places where clumps of the tree *Prosopis spicigera* are found, together with a few date palms. The commonest bushes are *Calligonum comosum* and *ghadha* (a kind of tamarisk), and *Leptadenia spartium* also occurs. These bushes are quite abundant in places, but there are large stretches with very few or none. All the vegetation was fresh and green during the author's journey, and the sand was moist from 3 ins. below the surface as far as the arm could reach.

Within about 5 miles of Bareimi, there is a flat plain of hard *sih* ground with hummocks of sand on it, which continues up to the foothills, just behind the villages of Bareimi. This plain contains patches of trees, *Acacia tortilis*, *Lycium persicum* and *Prosopis*, and a much denser growth of annuals than the sands. The following species are common : *Arnebia hispidissima*, *Silene villosa*, *Sisymbrium erysimoides*, *Cleome arabica*, *Centaurea pallescens*, *Ruta tuberculata*, *Plantago albicans*, *Arnebia cornuta*. The undershrub *Salicornia fructicosa* is abundant. There is a wady flowing south-west from the hills at Bareimi, and springs from which dates, and some grains and fruit trees are irrigated.

Similar cultivation to this exists at Ras el Kheima in the east, which is also near the hills where they approach the coast. It presumably occurs all along the edge of the hills. On the coast, a few date gardens are to be found near the towns, but in the Oman sands the author saw only a few date palms in certain places where there is ground-water. These are not tended, but the fruit is collected by the owners when it ripens. There is a settled area known as Lewi, south and west of the most westerly point visited by the author, which has villages and more cultivation. South-west of Bareimi, there are higher dunes with less vegetation. There had been less rain in this area.

Locusts in the Trucial Coast Area.

No solitary locusts were found on the coast, and only three specimens in the Oman sands proper. These were in an area about 12 miles north-east of Bareimi, which had nothing to distinguish it from the rest of the sands.

In the plain near Bareimi described above, odd solitary locusts were to be found. The largest number were within two miles of the villages where the plain was open *sih*, with many hummocks of sand and *Salicornia fructicosa* bushes. Here 8–15 could be found in a mile. They were sexually mature adults presumably of the first winter generation, and were mostly *in copula* in March. A few could also be found in the wady at Bareimi where it spread out into the plain. Some patches of wheat grown in this area were examined, but no *Schistocerca* were found.

Conclusions on the Oman Area.

The above examples in the sands near Bareimi, and at Bareimi itself, and those near Sohar in the Batina plain, are the only instances in which any solitary desert locusts were found during the author's journeys in Oman.

With the exception of the coast south of Muscat, rains had been good everywhere when the examinations were made, and on the Trucial Coast exceptionallly good. One would, therefore, have expected to find solitary locusts numerous if they occurred at all. If they could not increase to a greater extent than was seen at Bareimi after a winter of heavy rains, one would be inclined to say that the area would never be an outbreak centre.

Oman, however, is different from the Red Sea coast principally in that it has a much colder winter. It resembles the Mekran coasts of north-western India more closely. Ramchandra Rao, who has been working in this area for several years with his collaborators, has formed a theory as to how outbreaks may originate in north-western India (1936, 1937). It will be advisable to summarise this theory here.

The coast north of Karachi is partly rocky and partly open. The open coastal plains contain sand dunes with more or less vegetation known as " reks." Most of this Mekran coast receives winter rains, and in the country inland the rains may continue until May. From Ambagh southwards and eastwards, the rainy season is the monsoon.

Solitary locusts breed in these various places during their respective rainy seasons. It was noticed that sudden increases of population, which could not be accounted for except by an immigration, occurred in different places at various times. Conversely, sudden decreases in the population would take place.

Ramchandra Rao's theory is briefly as follows: Adults which have bred on the coast in the winter may emigrate individually at the beginning of the hot weather (April), possibly owing to climatic changes. They are carried inland by the wind, and may concentrate near patches of cultivation in the inland valleys. If these parts receive late rains, the locusts will breed near these patches of cultivation and their offspring will be phase *congregans*.

If solitary locusts behave like this in India—and there is strong circumstantial evidence in support of the theory—they might well do the same in Oman. Pending more detailed investigations, therefore, we must regard Oman as a possible outbreak area.

General Conclusions.

If we refer to the list of the sandy areas of southern Arabia on page 607, we can now see what conclusions can be arrived at with the brief evidence at our disposal.

1. *The Ruba' el Khali and its borders.*—The Ruba' el Khali itself has probably too low a rainfall and is too uniform (Philby ; Thomas) to contain outbreak centres.

Its south-western borders, including the wadys such as Beihan and Hadramaut, have probably insufficient rainfall.

The north-eastern borders towards the Oman mountains (*e.g.*, Bareimi) have some suspicious features.

The north-western and south-eastern edges have not been seen by the author.

2. *The Dahna* and sandy areas in southern Nejd have not been investigated. It was proposed to visit this country at the end of the author's last tour, but the project had to be abandoned for financial reasons.

These areas are not strongly suspected of being important, but an investigation should be made if the opportunity offers. The spring (April) would be the best time for a visit to be made.

3. *The Oman coasts* and the interior up to the foothills must be regarded as under suspicion and requiring further investigations. The interior may receive some monsoon rain, so that a visit in August would be useful, with another in April. If there was no sign of an outbreak after two exceptionally good rainy seasons, we might be justified in ignoring this area in future.

4. *The south coast.*—The part of the coast which was investigated (from near the Bab el Mandeb to Ahwar) has features which render it suspicious. Further investigations are needed and would need to be carried out in May, September and January. It would be impossible to reach any conclusion until the area had been inspected during at least one good rainy year.

The long stretches of the south coast to the east of Ahwar are very little known, and should certainly be investigated.

5. *The southern part of the Red Sea coast.*—The stretch from El Lith to Jizan is undoubtedly an outbreak area, and this probably applies also to the coast of the Yemen.

These rather vague results are the outcome of the author's 12 months' journeyings in Arabia. Unfortunately, travel in Arabia entails a deplorable amount of delay, so that the time for the actual work was all too short.

Investigations on the Desert locust have been carried out by French, British and Indian entomologists for the past six years and certain definite results have been obtained. Large regions have been found to be purely invasion areas, in which outbreaks cannot originate, and only certain small areas have been proved to contain outbreak centres.

It has also been shown that outbreaks of *Schistocerca* can be suppressed at their source by the ordinary means of poisoned baits. Such outbreaks were suppressed for example in Tokar District of the Anglo-Egyptian Sudan during three successive years by the District Commissioner and staff.

Now that the problem of controlling the Desert locust has been elucidated to a certain point by entomologists it has reached a stage where practical measures should be inaugurated. Such measures should necessarily be on an international scale. In order to enable an international control organisation to be set up, two main difficulties will have to be overcome.—

1. The richer Governments of the countries subject to invasions must agree to subscribe an annual sum, sufficient to establish and maintain a permanent anti-locust organisation.
2. The poorer Governments, if they cannot subscribe, must agree to control measures being carried out in their territories, and offer every facility to the organisation.

Once the organisation was functioning, the entomologists in charge would be in a position to carry out further investigations in addition to the routine work of patrolling known outbreak areas and suppressing incipient swarms. This would enable the outbreak areas to be defined more accurately, which is needed particularly in the case of Arabia.

If such an organisation can be started and put on a permanent basis, there should be every hope of preventing the Desert locust from spreading beyond its outbreak areas.

Acknowledgments.

The author offers his thanks to the following :—

The Government of Saudi Arabia for facilitating his journey on the Red Sea coast and for providing free transport.

The Government of Aden for arranging many journeys in the Protectorate, and the No. 8 Bomber Squadron R.A.F. for much transport. The Sultan of Laheg, the Sultan of Mukalla and many Aden Protectorate Sultans and Sheikhs.

The Resident of the Iranian Gulf and the Political Agents of Bahrein and Muscat ; the Sultan of Muscat, Syed Shahab and Captain Byard ; the Residency Agent at Sharja ; the Sheikhs of the Trucial Coast, especially Sheikh Shakhbut of Abu Dhabi ; and the Sheikh of Bahrein and Mr. Belgrave, for assisting me in various ways.

Mr. Ramchandra Rao for a trip to Ambagh and much kindness at Karachi ; and Dr. B. P. Uvarov for much help.

The Director of the Herbarium, Kew, for identification of plant specimens.

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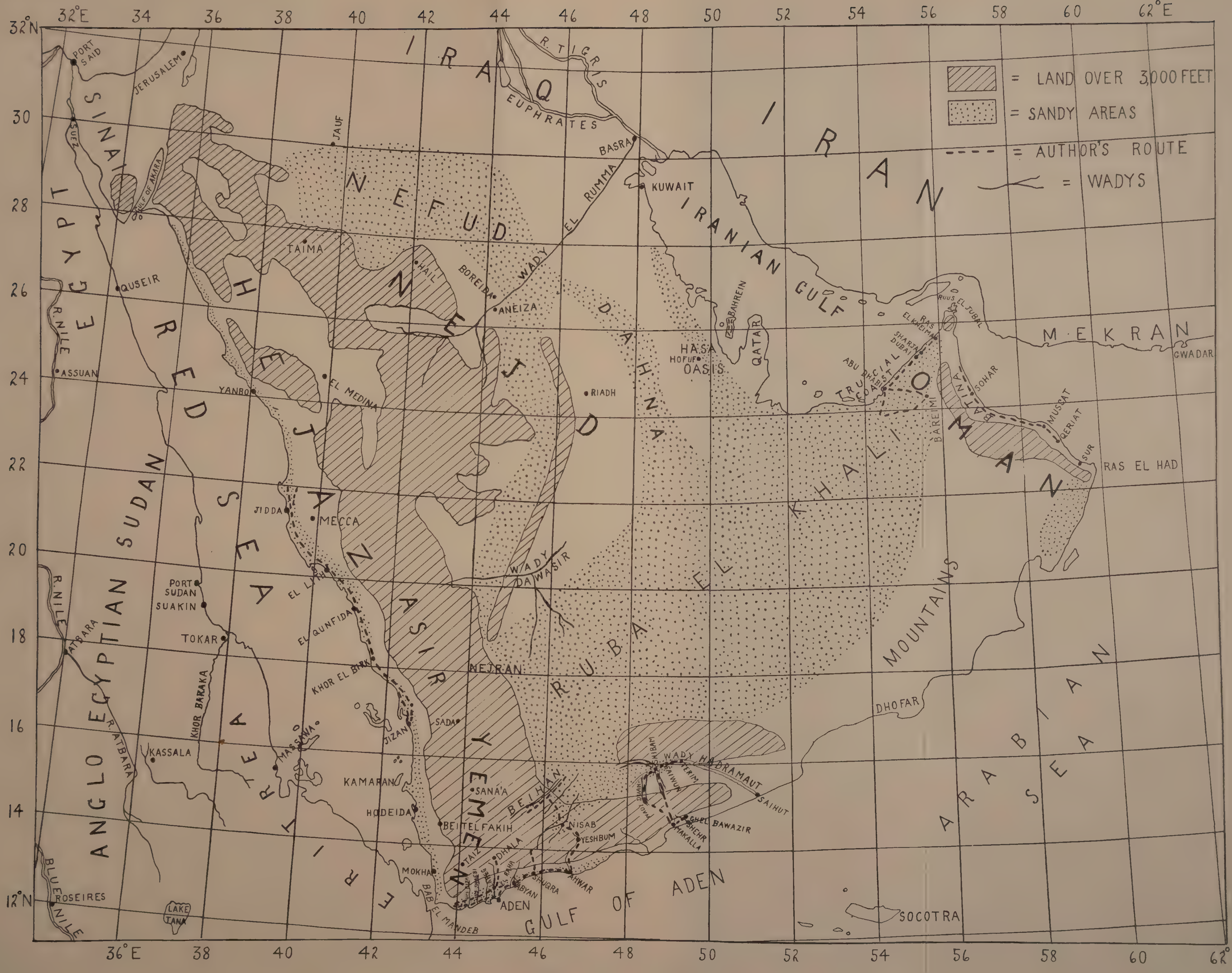
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= LAND OVER 3,000 FEET
= SANDY AREAS
= AUTHOR'S ROUTE
= WADYS
IRAQ
IRAN
R. TIGRIS
EUPHRATES
BASRA
KUWAIT
IRANIAN GULF
PORT SAID
JERUSALEM
SUEZ
SINAI
GULF OF AKABA
EGYPT
QUSEIR
R. NILE
ASSUAN
JAUF
NEFUD
TAIMA
HAIL
BOREIDA
ANEIZA
WADY EL RUMMA
NEJD
DAHNA
HEJAZ
RED SEA
YANBO
EL MEDINA
JIDDA
MECCA
RIADH
BAHREIN
QATAR
HASA
HOFUF
OASIS
RUUS EL JIBAL
RAS EL KHEIMA
SHARJA
DUBAI
ABU DHABI
TRUCIAL COAST
BAREIMI
BATINA
SOHAR
MUSCAT
QERIAT
SUR
RAS EL HAD
MEKRAN
GWADAR
OMAN
RUB AL KHALI
MOUNTAINS
WADY DAWASIR
ASIR
NEJRAN
EL LITH
EL QUNFIDA
KHOR EL BIRK
SADA
JIZAN
KAMARAN
HODEIDA
BEIT EL FAKIH
SANA'A
YEMEN
BEIHAN
MOKHA
BAB EL MANDEB
TAIZ
DHALA
ADEN
ABYAN
SHUQRA
AHWAR
NISAB
YESHBUM
SHIBAM
WADY HADRAMAUT
TERIM
SAIHUT
GHEIL BAWAZIR
SHEHR
MAKALLA
GULF OF ADEN
DHOFAR
ARABIAN SEA
SOCOTRA
SUDAN
PORT SUDAN
SUAKIN
TOKAR
ATBARA
R. NILE
ANGLO EGYPTIAN SUDAN
KHOR BARAKA
R. ATBARA
KASSALA
MASSAWA
ERITREA
BLUE NILE
ROSEIRES
LAKE TANA

SKETCH MAP OF ARABIA.

Explanation of Plate XVII.

Fig. 1.—Plain near Bareimi. Hard *sih* with *Arnebia hispidissima* and mounds of sand with bushes of the succulent *Salicornia fructicosa*. In the background are the palms of Bareimi.

Fig. 2.—Wady Hadramaut near Shibam. Wide sandy valley flanked by high limestone cliffs. The actual Wady bed is behind the houses. Palms, wheat and lucerne are grown. All the cultivation visible is irrigated, as there has been no flood.

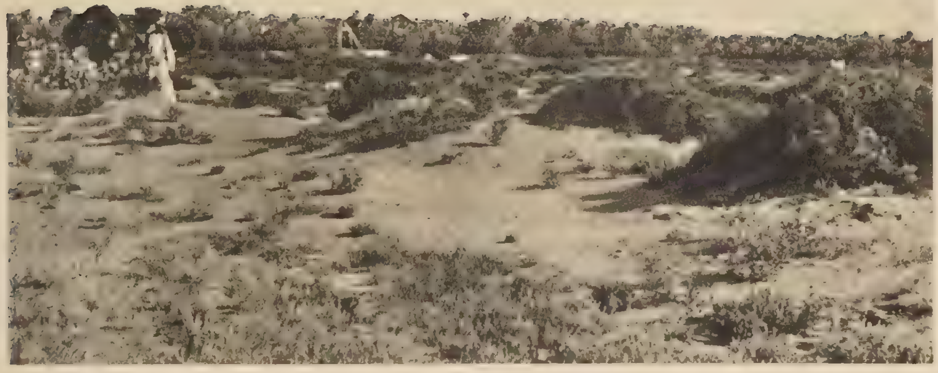

Fig. 1.

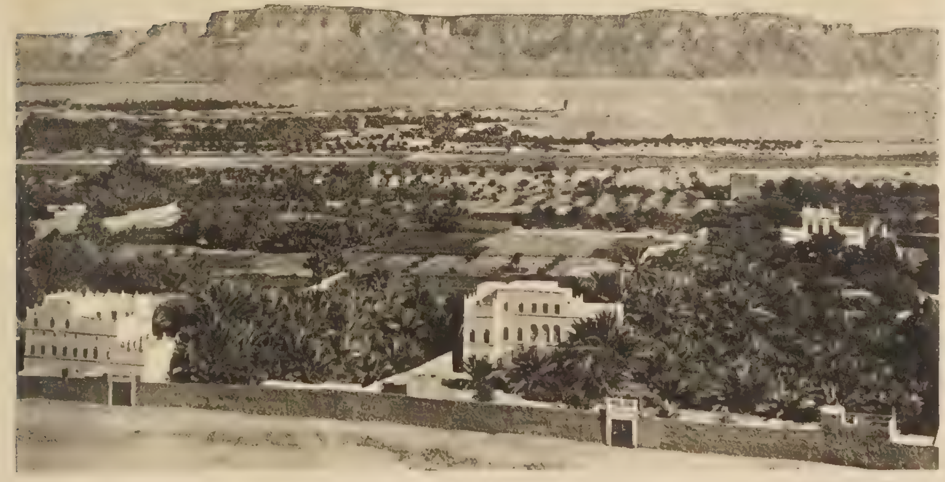

Fig 2.

STUDIES ON THE RED BOLLWORM OF COTTON, *DIPAROPSIS CASTANEA*, HAMPSON.*—PART I. THE DISTRIBUTION AND ECOLOGY OF TWO NATURAL FOOD-PLANTS, *CIENFUEGOSIA HILDEBRANDTII*, GÜRKE, AND *GOSSYPIUM HERBACEUM* VAR. *AFRICANA*, WATT.

By J. Marshall, F. S. Parsons & H. Hutchinson.

(Plates XVIII, XIX and Map.)

Introduction.

The present paper reports the principal results from a survey undertaken with the objects of ascertaining the extent of the natural breeding areas of the red bollworm in South Africa and whether the habitats of the food-plants are well defined ecologically. It has been known for some years that the red bollworm feeds on wild cotton, *Gossypium herbaceum*, and on *Cienfuegosia Hildebrandtii* (Parsons[8]), but from increased knowledge of the topography and vegetation of the country there were reasons to suppose that the distribution of these food-plants is quite considerably limited in the present and potential cotton-growing areas, and it was desirable that the situation should be investigated in some detail.

These studies were complementary to other work, to be communicated in Part II of this series, on the relationship of the bollworm with its natural food-plants, wherein, amongst other considerations, eradication of the plants is envisaged. A definition of habitats would facilitate other investigations, would conduce towards organized eradication, and would assist greatly in determining the limits of distribution.

Hibiscus calycinus, Willd., and *Cienfuegosia Gerrardii*, Harv., have been reported by us (Parsons[7]; Hutchinson[5]) to be natural food-plants of *Diparopsis castanea*. Subsequent examinations have shown, however, that although eggs are deposited very occasionally on them, the larvae have failed to mature, and they are not now regarded as food-plants. In the course of the present survey it has been necessary to re-examine and tabulate the flora (*vide* Appendix II) and it may be stated with some confidence that in the areas discussed the natural food-plants are confined to the two given in the title, with the possible exception of *Thespesia* spp. on the coastal fringe of Zululand and Portuguese East Africa, a possibility that has not been explored sufficiently; *Thespesia* has never been confirmed, however, as a food-plant elsewhere.

Monteil[6] states that *D. castanea* feeds on *Hibiscus cannabinus* in French Equatorial Africa and Russo[9] that the bollworm infests cotton and other unspecified Malvaceae in Italian Somaliland. In the literature there are numerous references to natural breeding on wild and semi-wild types of *Gossypium* in Africa.

As the red bollworm is a pest of cotton or is known to be present in some part or other of most of the cottton-growing countries in Africa, it may serve a useful purpose to denote the known occurrence (in Africa) according to Burtt Davy[1], Harland[4] and others with our additions, of three species of *Cienfuegosia*† and

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* Contribution from the Cotton Insect Pest Control Section, Cotton Experiment Station of the Empire Cotton Growing Corporation, Barberton, South Africa.

† Skovsted[10] mentions that Africa apparently contains the following species of *Cienfuegosia*:—*C. Dinteri*, Ulb., *C. Ellenbeckii*, Gürke, *C. somalensis*, Gürke, *C. Bricchettii*, Ulb., and *C. triphylla*, Harv., adding that these five species are indistinguishable from the genus *Gossypium* in its present demarcation (Skovsted's classification of the genus is based on cytological studies). The authors have been able to obtain little or no information concerning their distribution in Africa.

G. herbaceum var. *africana* and other types of indigenous or early-introduced cottons; the designations of the cottons being taken from Harland's classification in the Genetics of *Gossypium* (*l.c.*).

Cienfuegosia digitata, Cav.; *C. digitata* var. *genuina*, Hochr.*

Occurrence.—The Rustenburg and Waterburg Districts between Zoutpansberg and the Limpopo River in the Transvaal, N'gamiland, Bechuanaland, Southern Angola, Upper Guinea and Senegal. The plant has not been observed by the authors. It may serve as a food-plant of *D. castanea* in the portions of the Transvaal named and in the other regions given, but to the authors' knowledge it has not been so reported.

Cienfuegosia Hildebrandtii, Gürke.

Occurrence—Zululand, the Eastern Transvaal and Swaziland. Portuguese East Africa—between the Incomati and Maputa Rivers in the South. In the Zambesi River Valley between Chinde on the coast and a point approximately 20 miles south-west of Port Herald, Nyasaland. It is also reported, in a personal communication by Senhor Armando Salbany, a cotton experimentalist familiar with the plant and the country, to occur on the coast near Moçambique. Southern Tanganyika (Burtt Davy). Southern Rhodesia—the Zambesi Valley.

The occurrence in the Valley within Rhodesia must be some 200–300 miles westwards of the location near Port Herald. The presence of the food-plant in this region is of particular importance with regard to projects of native-grown cotton on the Northern Rhodesia side of the Zambesi and in the valley of the Loangwa River, which joins the Zambesi at a common boundary point of the two Rhodesias with Portuguese territory.

Cienfuegosia Gerrardii, Harv.

Occurrence—The species is reported only from the middle veld districts in the Union of South Africa and in Swaziland. It is to be found on the easterly margin of these districts which Burtt Davy (*l.c.*) places in his Eastern Mountains botanical province.

For convenience of reference a Key to the genus, as provided by Burtt Davy, is given in Appendix I, and *C. Hildebrandtii* is illustrated in Plates XVIII, fig. 1, and XIX.

The only wild cotton of the eastern areas of South Africa and the southerly portions of Portuguese East Africa is apparently *G. herbaceum* var. *africana* (frequently cited as *G. obtusifolium*, Roxb.). This type and variations of it extend far to the north on the easterly coastal belt of Africa and are distributed westwards to the Gambia and other regions of West Africa. In East Africa a Peruvian type of cotton is found along the former slave routes, and Burtt Davy, quoting from Watt, makes mention of a species in Mozambique "reminiscent of *G. Kirkii*," but Harland excludes this from the genus *Gossypium*. Other references from East and Central Africa relate apparently to *G. barbadense*, Linn. (including *G. peruvianum*, Cav., and kidney cotton, *G. brasiliense*, MacF.) or to *G. herbaceum* var. *Wightiana*, Watt. The latter, however, which Harland places in the Levant group, is of more frequent occurrence in North Africa, where it comprises, with *G. arboreum*, Linn., and forms of *G. herbaceum* var. *africana*, the wild and semi-wild cottons ranging from Eritrea through Abyssinia and the Sudan westwards. Watt[12] considers the Sennaar cotton of Egypt to be *G. arboreum* var. *soudanensis* and possibly the "beledi" of the Sudan may be designated similarly.

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* It is highly probable that *C. digitata* occurs on the edge of the Kafue River Flats in Northern Rhodesia; specimens recently taken there by our colleagues, Mr. E. O. Pearson and Mr. Bebbington, are stated by the former to agree with Burtt Davy's description of the species.

In the cotton-growing countries of West Africa members of the Bourbon and Peruvian groups predominate, notably *G. punctatum*, Sch. & Thon., and the Ishan cotton of Nigeria.

Such specific references as there are in the literature to the natural breeding of *D. castanea* concern one or other of the wild or semi-wild cottons alluded to in addition to the *Cienfuegosia* and *Hibiscus* species reported by ourselves and Monteil. The association of the moth with cultivated and wild food-plants is confined very narrowly within the natural order Malvaceae, and it would be helpful in studies of the bases of the relationship if the botanical designations were given when food-plants are reported rather than local and vernacular names.

The information presented below was obtained from a survey of Swaziland, Zululand and the Eastern Transvaal as far north as the Olifants River.

Physiography.

According to altitude the country surveyed may be divided into strips of variable width running north and south. This is illustrated well in the map which has been prepared from the Topographical Survey Sheets of the Union of South Africa. That portion on the west at elevations over 4,000 ft. is unsuitable for cotton-growing in this climate ; its eastern boundary marks the edge of the High Veld and, as viewed from the east, generally presents a mountain-like aspect. For the purposes of this discussion we may term the country within the 2,000–4,000 ft. limits as " Middle Veld," that within 1,000–2,000 ft. as " Upper Bushveld," and below 1,000 ft. as " Lower Bushveld." These divisions are appropriate, as they accord to a considerable extent with changes in vegetation and climate.

The Middle Veld is in part rolling and valley country, but the region is so traversed and studded with hilly masses that agricultural land is limited and farming communities are widely separated. It contains, however, the greater portion of the present-day cotton-growing areas and, with a marginal portion of the Upper Bushveld, the largest potential cotton areas available for dry-farming conditions.

The Upper Bushveld on the western side (1,400–2,000 ft.) is a much dissected region of granitic ridges, strings of kopjes and isolated rocky masses. Agriculture here is confined largely to the valleys of rivers and streams or to occasional patches of higher land where the granite is overlain or has been modified by admixture with components from other sources. At lower levels the country tends to a more uniform aspect, but the soil is of a thin, stony nature. This is true particularly of the broad band of the Upper Bushveld that is shown on the map to the north. At points on the easterly margin of this sector, however, where the descent is more gradual, the granite disappears beneath the sediments of the Karroo system and good soil conditions obtain.

The Lower Bushveld extends to the Indian Ocean but is divided along the 32nd Parallel of Longitude by the Lebombo Mountains, a narrow, basaltic range extending from upper Zululand to the Sabie River, northwards.

Along the whole length of the Lebombos on the westward side there is a plain of variable width known as the Lebombo Flats. At points the Flats extend to the verge of the Upper Bushveld, but generally speaking there is an intervening belt of somewhat broken country which merges with the lower portions of the Upper Bushveld.

The soil of the Flats and their immediate neighbourhood is derived from the sandstones and sediments of the Karroo System with additions from the basaltic lavas of the Lebombo Mountains ; it is rich and deep but, owing to the deficient rainfall of recent years and damage by insect pests, cotton-growing has not prospered there.

On the seaward side the Lebombos dip to the east beneath the deep soil of extensive plains formed from Marine Beds followed by a wide costal belt of sand. Little European agriculture has been attempted in this tract, but in view of irrigation projects referred to later, a part of it was included in the survey.

The survey was particularly intensive in the Valley of the Pongola River and in the neighbouring Magut Valley, as both have been important areas of rain-grown cotton. The work there was complementary to observations (*cf.* St. Phillip's Mission) on the breeding cycle of red bollworm in the Pongola Valley, where under an established irrigation scheme experiments are in progress on evading pests by growing cotton in the dry season.

Procedure and Treatment of Data.

The vastness of the area precluded any hope of carrying out a detailed analysis of the vegetation, examination of soils and other factors, except in the neighbourhood of widely separated situations, of which several were taken in the Upper and Lower Bushveld and others centred upon the cotton experiment stations or farming communities in the Middle Veld districts. Examination of the environment between the selected points and along divergent routes was attempted in a more general manner ; the disposition of the points and routes taken is indicated in the map. The survey occupied three months of field work, and 4,000 miles were travelled by road, exclusive of traverses afoot.

The survey started at St. Phillip's Mission, in the Lower Bushveld of Swaziland, which was particularly suitable as both food-plants occur there in abundance, and also because a field station was established near by a year ago for investigation of the bionomics of the red bollworm in the natural breeding area afforded by the presence of these plants.

Plant associations were obtained by taking counts of all trees, shrubs and the principal grasses in simple traverses that were each about five yards wide and a mile long. In places where an intensive survey was made these traverses were spaced at intervals over many square miles, and we estimated that 0·3 per cent. of the terrain was viewed and recorded. The native names of all plants were used in the tallies taken, as they enabled more rapid progress ; cross-traverses were attempted wherever possible. It is believed that in this way an adequate sample of the vegetation was procured and, although the procedure varied somewhat according to local conditions, the above system was the basis for all the work. In the country between the points of detailed study traverses were undertaken and plant associations were investigated closely only where colonies of the food-plants were observed.

In conjunction with the above botanical analyses extensive notes were prepared on topographical details, soil and rock samples were collected, and occasional profiles and root systems were examined in order to complete the information. Gadd's method[2] for the determination of pH values colorimetrically and Hardy's technique[3] for the expression of other characteristics were employed in laboratory tests of the soils collected.

The data obtained from the large number of traverses supplied ample material for recognition of the abundance and distribution of the species occurring. These data were collated according to the system of Tansley & Chipp,[11] where they term the numerical occurrence of any species the *abundancy* of that species and the frequency with which any species occurs in the different samples the *constancy* of that species. Five grades of both *abundancy* and *constancy* are recognized and they are assigned the digits 1 to 5, where 5 is the maximum value. Thus having obtained the list of species present, the information when treated in this manner becomes tabulated and the *abundancy* index supplies the population value for each species and the *constancy* index supplies the frequency of its distribution throughout.

It should be stated here that as the survey proceeded altimeter readings revealed that neither food-plant is present above 1,200–1,300 ft. elevation. They are indeed rarely found above 1,100, and are numerous only at lower levels. The evidence on this very important point was confirmed abundantly, and reference to the map and remarks in the section on physiography will show that we may on the score of altitude at once exclude from the habitat all of the Middle Veld and practically all of the Upper Bushveld. The excluded areas embrace the cotton-growing districts of mid-Swaziland, the Barberton (or De Kaap) Valley and other mid-country cotton districts of the Eastern Transvaal, or in fact the greater portion of the present-day cotton areas. The included areas all lie within the Lower Bushveld and a marginal portion of the Upper Bushveld, hence the information presented below derives from investigations there.

Plant Associations in the Lower Bushveld.

General.

Except at points where the conditions are modified profoundly by exposure, soil factors and proximity to water, the vegetation of the Lower Bushveld south of the Crocodile River fluctuates between dense thickets of *Acacia* thorn shrub, undulating *Acacia* savannah and grassy open parklands where the larger trees are found. Appreciable differences in " types " of vegetation do occur, but particulars of these may be omitted as attention was directed primarily to the associations found in environments containing the two food-plants under review. In all, the distribution of 100 species of trees and shrubs was tabulated ; these occurred substantially in all situations, though in differing quantities, those met with most commonly being *Ormocarpum setosum*, *Ehretia rigida*, *Acacia litakunensis*, *Dichrostachys glomerata*, *Spirostachys africana*, *Acacia heteracantha* and *Commiphora* sp.

A list of the main species occurring in two major sections of the region is given in Appendix II, grouped in terms of *abundancy* and *constancy*.

North of the Crocodile River and verging on Latitude 24° south the region of dominance of mopani (*Copaifera mopani*, Kirk) is entered, but, as explained later, *C. Hildebrandtii* was not found in this portion of the Eastern Transvaal, and in view of this and later remarks on the distribution of wild cotton, further comment on the general plant associations need not be made.

Plant Association in Cienfuegosia *Habitats.*

Information obtained from the system of traversing contributed largely to an understanding of the usual types of association. With this knowledge it was observed that in the immediate environment of *Cienfuegosia* dominance of certain plants was exhibited clearly, and from repeated counts at many sites the data in the following Table were assembled :—

Plant Association Table of Cienfugosia *Habitats expressed in Terms of Abundancy and Constancy.*

(Out of a total of 64 spp. recorded.)

Abundancy.	Constancy.
5. *Acacia barbertonensis.**	5. *Acacia barbertonensis.*
4. *Acacia heteracantha.*	4. *Acacia heteracantha.*
Aloe sp.	*Euclea lancifolia.*
	Gymnosparia sp.

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* Recently described by Dr. Schweickerdt (*Kew Bulletin* 1937, p. 448).

Abundancy.	Constancy.
3. *Gymnosparia* sp. *Acacia litakunensis.*	3. *Dichrostachys glomerata.* *Acacia litakunensis.* *Zizyphus mucronata.* *Aloe* sp. *Spirostachys africana.* *Ehretia rigida.*
2. *Euclea lancifolia.* *Ormocarpum setosum.* *Spirostachys africana.* *Ehretia rigida.*	2. *Cassine Schlechteri.* *Carissa bispinosa.* *Rhus spinescens.* *Ormocarpum setosum.* *Bolusanthus speciosus.*
1. *Cassine Schlechteri.* *Carissa bispinosa.* *Bolusanthus speciosus.* *Rhus spinescens.* *Zizyphus mucronata.* *Gossypium herbaceum* var. *africana.* *Dichrostachys glomerata.*	1. *Gossypium herbaceum* var. *africana.*

An intimate association of the food-plant with *Acacia barbertonensis* was established by the counts and by all subsequent observations. *Euclea lancifolia,* although less numerous than *A. barbertonensis*, was found in a very large percentage of the samples. These two plants are not restricted absolutely to the *Cienfuegosia* habitats, but they, particularly *A. barbertonensis*, proved to be most reliable indicators of the presence of *C. Hildebrandtii*. *A. barbertonensis* (Plate XVIII, fig. 2) grows in coppices that are remarked very readily in the leafless condition of the dry season, and the discovery of this indicator plant greatly facilitated the purposes of the survey. Although at times confused at a distance with another shrub, *Acacia swazica*, the two are readily distinguishable at close quarters on thorn and bark characters. Fortunately the survey concluded before the resumption of foliage, as it was then found that *A. barbertonensis* loses its outstanding appearance and several other species of *Acacia* may be mistaken for it unless examined closely. *Acacia heteracantha* and *Gymnosparia* sp. although both abundant and constant are too widely dispersed to serve as indicator plants.

G. herbaceum was infrequently in association with *Cienfuegosia.*

Distribution and Habitats of Cienfuegosia Hildebrandtii.

Apart from the aforementioned fact that the upper limits in nature of the plant's growth lie between 1,200–1,300 ft., the authors never found it in the thin, stony soils* which occupy perhaps 50–60 per cent. of the region of the Lower Bushveld (west of the Lebombo Mountains), and ultimately attention was focussed upon the areas of better and deeper soils. Repeated examinations there disclosed that the habitats of *C. Hildebrandtii* could be divided into three classes, (*a*) the crests and sloping sites of low elevations, (*b*) along water channels, and (*c*) pans (vleis) ; in the latter instance a distinction could be drawn between grassy, gravelly or silty pans and certain depressions with impervious clay bottoms.

Tracing the local distribution of the plant it became apparent that the water channel and pan occurrences were due to water-borne dissemination of seed from an upper point where existed more or less large and flourishing colonies of *Cienfuegosia,* and subsequent investigations confirmed the relationship. The evidence clearly indicated that the primary focus is one on the crests and slopes of low hills and eminences that have a good soil cover, the other occurrences being consequent on proximity to watercourses.

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* By contrast *C. Gerrardii* is found in colonies growing in scanty soil in the hilly ground above altitudes of 1,400 ft.

Although the Lower Bushveld appears from a height to be fairly level, it is in reality much and deeply dissected by rivers and tributary waterways, many of which deliver flood water through a series of pans. Additionally the plains are relieved by occasional low eminences and ridges and by long spurs rising in the east to the Lebombos or on the west to the hilly country in the Upper Bushveld. From the Upper Bushveld to the Lebombo Mountains and beyond there is an eastward descent of varying gradient. The source of rivers and streams is within the western uplands and, in the main, the upper reaches of subsidiary water-channels commence in the granitic, thin-soil areas where *C. Hildebrandtii* is non-existent. There are thus no upper colonies to furnish seed in a west to east direction until one enters the areas of modified granitic soils, the Karroo sediments, the Marine Beds or, in the south, the rich soils of the Pongola System, and for all practical purposes the distribution of the primary foci in this region is confined to the higher ground in these formations, and then only to points where good soil exists, a further limitation being access to moisture, generally alongside catchment areas. Such sites are not notably numerous west of the Lebombos and they are readily remarked with the aid of the indicator plants ; in fact it was possible to map the locations of colonies over the whole of the Pongola Irrigation Scheme and surrounding country, an area of approximately forty thousand acres.

Where streams and tributaries flowing in a generally eastward direction cross the above-mentioned formations they serve to disseminate seed. The water from streams and erosion channels having their rise in the western face of the Lebombo Mountains and from various aspects of other elevated ground in the Lower Bushveld frequently joins with the water from the west, and in any event all enters one or other of the rivers that at intervals of ten to thirty miles flow to the Indian Ocean through precipitous and narrow gorges in the Lebombo range. Quantities of seed find lodgement along this network of watercourses, particularly pans, and doubtless a proportion is carried through the mountains to the plains beyond, which are pre-eminently the home of *C. Hildebrandtii.*

The seed when ripe bears a short, brown fuzz (Plate XIX), is light and floats readily. The presence of the plant downstream is confined to the immediate banks of the water-course below the source of seed supply or to the banks of subsidiary channels ; the plants are not numerous there except on gentle slopes or where pan areas open out.

The colonies in the pan habitats * are of primary importance *numerically.* Many of the pans are the culminating points of several water-channels and, although the germination percentage of lodged seed and that from surviving plants is apparently very low, they are full of the food-plant and bollworm breeding is most extensive. This is particularly the case on the eastern side of the Lebombos before the sandy stretches are reached. There the pans in question are shallower and rain-water drains away readily through sandy and silty deposits with a low clay content ; the conditions are generally favourable for plant growth in contradistinction to other pans west of the Lebombo Range. Particular mention may be made of the circumstances between the Range and the Ocean from the reconnaissance point of view. There is as yet no cotton grown in this large tract of country (within British Territory) but, under a projected irrigation programme, cotton-growing is reported to be contemplated. The authors are familiar with a vast incidence of red bollworm on defunct cotton estates in similar Portuguese Territory to the north, and it is believed that the knowledge gained from the survey may be used to advantage in this connection.

The impervious clay pans alluded to (page 626) are not habitats. These are depressions void of plant growth and containing a deep body of highly colloidal clay and soil matter ; they are of common occurrence in the Lower Bushveld and hold water for long periods. The extent to which *Cienfuegosia* abounds in other types of pans depends on the depth and permeability of the water-lain soil. Where the gradient is slight, the clay-silt fraction is very high centrally, leading to semi-impervious conditions, and the plant is restricted to the margins, particularly where the seed is eddied amongst debris. The soil in the higher pans being compounded of the heavier particles has a more open texture and supports the largest colonies.

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* Where the bush surrounding a pan is very thick *Acacia barbertonensis* is not found in association with *C. Hildebrandtii.*

As found on excavations the plant has an extensive root system and one which penetrates deeply into the permanently moist layers. It is thus well able to withstand the arid seasons and fruits regularly.

Apart from obvious requirements of depth and permeability in the soil habitat, examinations *in situ* and of some 140 samples in the laboratory did not reveal any specific relationship with static characteristics. The soils all gave an alkaline reaction with normal and reaction values ranging from *pH* 7·0 to *pH* 7·8.*

So far as we have been able to discern, the plant is not present in the Union (although it is in Portuguese East Africa) between the Crocodile and Olifants Rivers except in a small tongue of the Karroo sediments along the Lebombo Range near the confluence of the Crocodile and Komati Rivers. Dissemination by water from this point, except into Portuguese Territory, is barred by natural obstacles northwards and westwards, and in any event the soil in those directions is too thin to be favourable for the plant.

Distribution and Habitats of Gossypium herbaceum *var.* africana.

The main conclusion from our survey is that the plant appears to flourish indiscriminately with regard to both habitats and plant associations. Occasionally it is encountered in large and fairly well-defined colonies in situations with no comparable features, except that like *C. Hildebrandtii* they *all* lie within or on the verge of the Lower Bushveld. Large aggregations of wild cotton are exceptional, however, and commonly the plant is to be seen only in small scattered clumps or as isolated occurrences. The natives state that the seed is swallowed by antelopes and cattle, which may explain the somewhat haphazard distribution.

Although widely distributed co-extensively with the warmer, drier regions of the Lower Bushveld, *Gossypium herbaceum* is by no means abundant apart from the colony situations, and as these are readily remarked when the plants carry ripened bolls in the dry season, it would not appear to be an impossible or, indeed, a difficult task to eradicate them within and around a cotton-growing district.

Unlike *C. Hildebrandtii* the wild cotton also flourishes in the thin soils ; thus we find it over a much wider area and particularly north and north-west of the Crocodile River, where it is apparently the sole natural food-plant.

Discussion.

The objects of the survey, the nature of the country traversed and the principal results, have been communicated in the foregoing with the least detail and the findings with respect to red bollworm problems in South Africa are outlined briefly below.

The aim of the work is to counter the bollworm in the several cotton districts according to knowledge of the origin and development of infestations. We may now designate certain portions of the Lower Bushveld as the natural breeding-grounds of *Diparopsis castanea*, whether feeding on *C. Hildebrandtii* or on *G. herbaceum*, and because the aforementioned food-plant is coincident with agricultural lands below approximately 1,200 feet elevation, it follows that there cotton is cheek by jowl with the largest reservoirs of naturally-bred red bollworm ; wild cotton, where aggregated, contributing to an important degree.

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* Some of our colorimetric values were confirmed by quinhydrone electrode determinations carried out by Mr. B. P. Campbell, Natal Estates Ltd., Mount Edgecombe, whose help in this respect the authors gratefully acknowledge. Mr. Campbell advised that considerable drift was observed in the readings, due probably to the presence of manganese dioxide in the soils.

Under existing conditions the cotton-grower of the Lower Bushveld is faced with constant infestation and damage unless he may circumvent the red bollworm by (*a*) alteration of planting and growing season for cotton, or (*b*) eradication of the natural food-plants coupled with a rigid close season in each cotton-planting year. With regard to (*a*) the season for rain-grown cotton permits of no alteration and the possibilities thereof concern only the grower with irrigation facilities, and in how far or how successfully any possibilites may be applied depends largely on two things now being studied, namely, the progress of the cotton plant under irrigation in the dry season period and the course of fruiting and infestation of the natural food-plants, together with a full knowledge of the span of moth emergence. In the case of (*b*) it is now deemed practicable to carry out the measures conveyed, given the initiative and co-operation of cotton-growers made acquainted with the habitats.

The red bollworm is not a devastating pest in the sense that the American bollworm (*Heliothis armigera*) occasionally is, but the damage it causes deters cotton-growing in years of low prices, and it was a weighty factor in determining the abandonment of the cotton crop over large areas in the Lower Bushveld. It remains to be seen how far the red bollworm situation may be ameliorated in established cotton areas of this region, which are also the natural home of the pest.

Perhaps the most important result of the survey was the finding that natural food-plants are absent in the tracts which embrace the whole of the mid-country cotton areas. The bollworm has been introduced into all but one of these tracts and the problem is resolved into one of reducing the pest to a minor status ; on bionomical and other evidence, to be reported later, there is much hope of accomplishing this if cotton-growers will impose an annual close season.

The survey disclosed that there are portions of the Low Country where *C. Hildebrandtii* does not exist and problems of eradication concern wild cotton only.

Reference has been made to reconnaissance before development of the region between the Lebombo Range and the Indian Ocean, where immense colonies of *C. Hildebrandtii* and very considerable quantities of wild cotton are present ; here eradication would seem an impossible task and hopes of evading bollworm would rest on the success of irrigated cotton in the dry season.

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APPENDIX I.

Cienfuegòsia, Cav. (*Fugòsia,* Juss.), Flora of Tropical Africa 1, p. 208.

1 (2).—Leaf-blades palmatisect to the base, 3- (rarely 5-) fid; lateral lobes pinnatifid to simple, central lobe 3-fid to simple; stem annual, herbaceous from a woody rhizome; stipule 0·5 cm. l., not foliaceous; calyx 1·3 cm. l., lobes narrow acuminate 1·1 cm. l.; corolla 2·2 cm. l .... *digitata.*

2 (1).—Leaf-blades sub-simple to shallowly-lobed; stipule foliaceous, 1–1·5 cm., l.; corolla 4 cm. l.; stem perennial woody.

3 (4).—Leaf-margin toothed at the ends of the primary and secondary nerves; young stem and petiole hairy with simple hairs; stipule semi-ovate cordate, mucronate; leaf-blade cuneate at base; calyx 1 cm. l., lobes 0·4 cm. l., triangular mucronate..................................*Hildebrandtii.*

4 (3).—Leaf-margin entire, or undulate but not toothed; young stem and petiole scurfy or with a few scattered stellate hairs; stipule broadly linear, obtuse; leaf-blade cordate at base; calyx 1·3 cm. l., lobes 0·7 cm. l., lanceolate-acute ....*Gerrardii.*

APPENDIX II.

Plant Association in Two Major Sections in the Lower Bushveld, expressed in terms of abundancy and constancy.

Section I.

(Out of a total of 89 spp. recorded.)

Abundancy.	Constancy.
5. *Ormocarpum setosum.*	5. *Acacia heteracantha.*
Dichrostachys glomerata.	*Acacia litakunensis.*
Croton grassimus.	*Dichrostachys glomerata.*
Aloe sp.	*Ormocarpum setosum.*
Ehretia rigida.	*Gymnosparia* sp.
	Acacia pallens.
	Combretum sp.
	Zizyphus mucronata.
	Spirostachys africana.
	Euclea lancifolia.
	Bolusanthus speciosus.
	Commiphora sp.
	Olea woodiana.
	Gossypium herbaceum var. *africana.*
	Ehretia rigida.

SECTION I.—*continued*.

Abundancy.	Constancy.
4. *Spirostachys africana.* *Commiphora* sp.	4. *Euclea* sp. *Gymnosparia* sp. *Combretum* sp.
3. *Acacia heteracantha.* *Acacia pallens.* *Zizyphus mucronata.* *Gymnosparia* sp.	3. *Acacia barbertonensis.* *Croton gratissimus.* *Peltopharum africanum.* *Sclerocarya caffra.* *Aloe* sp.
2. *Acacia litakunensis.* *Gossypium herbaceum* var. *africana.* *Euclea lancifolia.* *Acacia barbertonensis.* *Rhus spinescens.* *Bolusanthus speciosus.* *Olea woodiana.* *Acacia Karroo.*	2. *Acacia swazica.* *Rhus spinescens.* *Balanites Maughamii.*
1. *Sclerocarya caffra.* *Peltopharum africanum.* *Carissa bispinosa.* *Schotia brachypetala.* *Sarcastemma viminale.* *Mundulea sericea.* *Sanseviera thyrsiflora.* *Balanites Maughamii.* *Acacia swazica.* *Euclea* sp. *Combretum* sp. *Gymnosparia* sp.	1. *Carissa bispinosa.* *Schotia brachypetala.* *Sarcastemma viminale.* *Mundulea sericea.* *Sanseviera thyrsiflora.* *Acacia Karroo.*

SECTION II.

(Out of a total of 86 spp. recorded.)

Abundancy.	Constancy.
5. *Acacia litakunensis.* *Gymnosparia* sp.	5. *Acacia heteracantha.* *Acacia litakunensis.* *Dichrostachys glomerata.*
4. *Acacia heteracantha.* *Aloe* sp.	4. *Ormocarpum setosum.* *Gymnosparia* sp. *Zizyphus mucronata.* *Ehretia rigida.*
3. *Ormocarpum setosum.* *Spirostachys africana.* *Dichrostachys glomerata.* *Ehretia rigida.*	3. *Acacia pallens.* *Sclerocarya caffra.* *Rhus spinescens.* *Spirostachys africana.* *Aloe* sp.
2. *Acacia pallens.* *Zizyphus mucronata.*	2. *Carissa bispinosa.* *Gossypium herbaceum* var. *africana.* *Euclea lancifolia.* *Acacia barbertonensis.* *Bolusanthus speciosus.* *Sanseviera thyrsiflora.* *Commiphora* sp. *Gymnosparia* sp. *Olea woodiana.*

SECTION II.—*continued.*

Abundancy.

1. *Sclerocarya caffra.*
Rhus spinescens.
Carissa bispinosa.
Gossypium herbaceum var. *africana.*
Euclea lancifolia.
Acacia barbertonensis.
Bolusanthus speciosus.
Mundulea sericea.
Acacia sp.
Commiphora sp.
Euclea sp.
Peltopharum africanum.
Olea woodiana.
Schotia brachypetala.
Sarcastemma viminale.
Sanseviera thyrsiflora.
Helichrysum erosum.
Cassine Schlechteri.
Acacia Karroo.

Constancy.

1. *Euclea* sp.
Peltopharum africanum.
Schotia brachypetala.
Sarcastemma viminale.
Sanseviera thyrsiflora.
Helichrysum erosum.
Cassine Schlechteri.
Acacia Karroo.

Grass Association.

Species found generally throughout the survey.

Panicum deustum.
Themeda triandra.
Digitaria sp.

Species found less frequently.

Arista congesta.
Eragrostis superba.
Cymbopogon plurinodis.

Species occasionally found.

Schmidtia bulbosa.
Pogonarthris squarrosa.
Eragrostis cilianensis.
Brachiara sp.
Tingerhuthia africana.
Chloris virgata.
Paspalum sp.

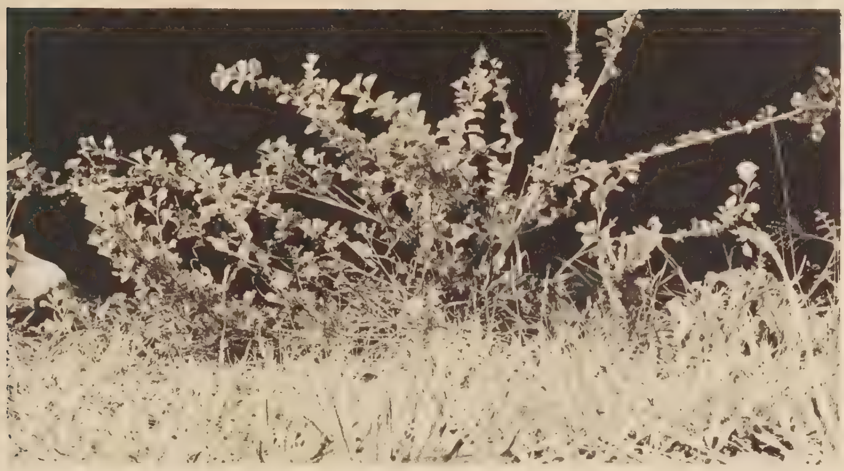

Fig. 1. *Cienfugosia hildebrandtii.*

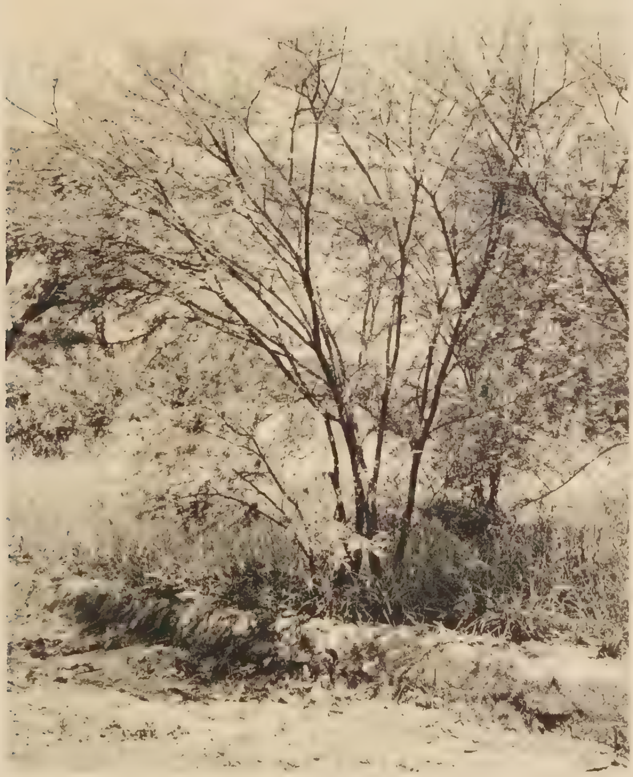

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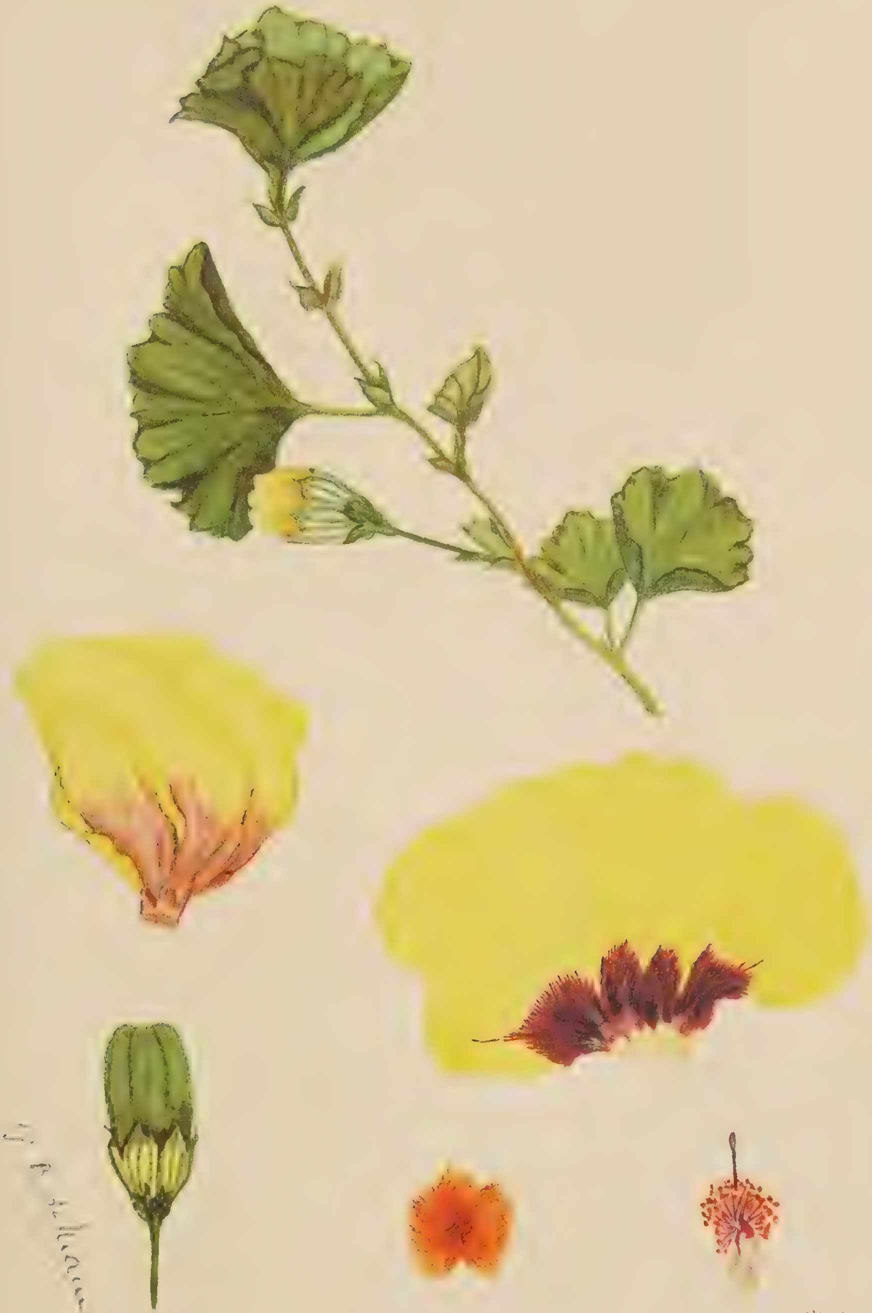
Fig. 2. *Acacia barbertonensis,* Schweickerdt, occurring in association with *Cienfugosia hildebrandtii.*



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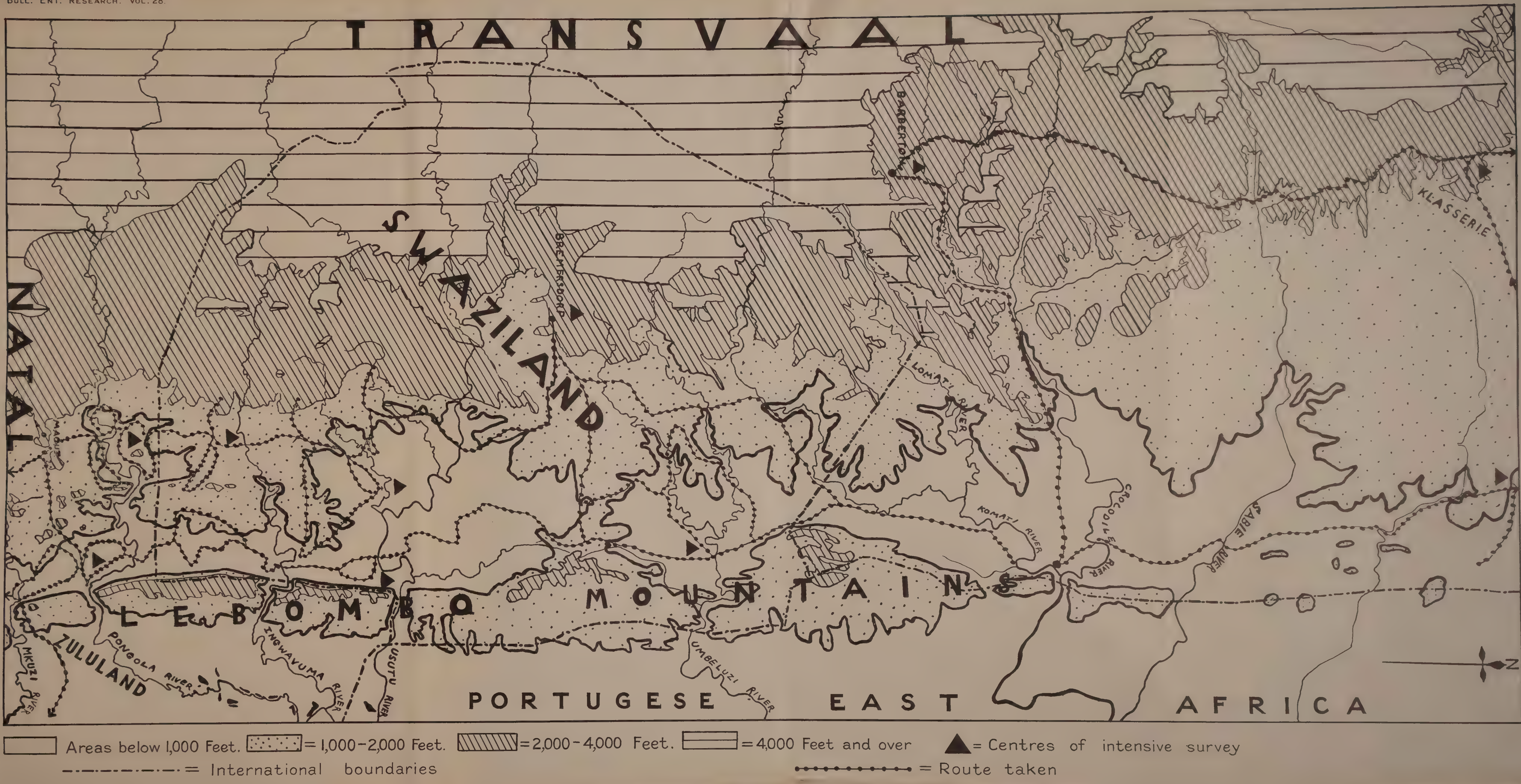
Cienfugosia hildebrandtii, Gürke.


TRANSVAAL
SWAZILAND
NATAL
ZULULAND
LEBOMBO MOUNTAINS
PORTUGESE EAST AFRICA
BARBERTON
BREMERSDORP
KLASSERIE
MAGUT
KOMATI RIVER
CROCODILE RIVER
SABIE RIVER
UMBELUZI RIVER
USUTU RIVER
INGWAVUMA RIVER
PONGOLA RIVER
MKUZI RIVER
N
Areas below 1,000 Feet.
= 1,000-2,000 Feet.
= 2,000-4,000 Feet.
= 4,000 Feet and over
= Centres of intensive survey
= International boundaries
= Route taken

THE FAUNA OF INJURIOUS SOIL INSECTS OF ARABLE LAND.

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Clean summer fallow is often recommended for reducing wireworm and white-grub infestations, but our investigations on this subject, conducted during the years 1933–35 at the Ukrainian Rubber Plants Experimental Station (near Kremenchug) showed that in arable fertile " chernozem " soil there is no significant decrease in the number of these pests after a clean summer fallow. These divergent results led us to suppose that the reaction of various species of wireworms and white-grubs to soil cultivation and fallow may be different.

In order to find out the relation of various species of injurious soil insects, occurring in the neighbourhood of the Experimental Station, to soil cultivation, the density of their population in the year 1935 was determined in cultivated fields that had been kept in clean fallow during the year 1934, and in conterminous plots of land abandoned for at least 8 years, on which couch grass, *Agropyrum repens*, was the most abundant weed.

Soil samples (50 × 50 cm., depth 40–50 cm.) were taken lengthwise along the margin of the arable and abandoned plots. The distance between each soil sample and the margin of the plot was approximately three metres, and from each field 18–40 soil samples were taken. Table I gives the results.

TABLE I.

Average Number of Soil Insects per Square Metre on conterminous cultivated and abandoned Fields, May 1935.

Field No.	1		2		3	
	Character of the Soil.					
Name of Insect	Arable, kept in clean fallow in 1934	Abandoned	Arable. kept in clean fallow in 1934	Abandoned	Arable, kept in clean fallow in 1934	Abandoned
Selastosomus latus, F.	0·0	5·82	0·57	4·57	0·0	2·0
Agriotes sputator, L.	4·5	4·73	4·57	1·71	0·8	0·4
Agriotes gurgistanus, Fald. ...	2·6	1·09	—	—	0·8	0·8
Omophlus proteus, Kitsch. ...	—	—	2·28	0·0	1·2	0·8
Podonta daghestanica, Reitt. ...	—	—	—	—	0·4	0·4
Tentyria nomas, Pall.	—	—	0·0	0·57	—	—
Asida lutosa, Sol.	—	—	0·0	2·23	—	—
Amphimallus solstitialis, L. ...	0·0	12·73	—	—	0·4	2·0
Anisoplia austriaca, Hbst. ...	2·5	0·0	0·57	0·0	2·0	0·4
Dorcadion spp.	—	—	0·0	9·71	0·0	12·0

The data obtained show that the wireworms, *Selatosomus latus*, the larvae of the chafer, *Amphimallus solstitialis*, the false wireworms, *Asida lutosa* and *Tentyria nomas*, and the larvae of *Dorcadion* spp., are more abundant in the uncultivated soil, while the wireworms, *Agriotes sputator* and *A. gurgistanus*, the false wireworms, *Omophlus proteus* and *Podonta daghestanica*, and the larvae of *Anisoplia austriaca* are as numerous in cultivated as in abandoned plots or are even more prevalent in the cultivated soil.

The same type of distribution of the wireworms, *Selatosomus latus* and *Agriotes sputator*, was registered in the year 1936 in Middle Russia, as shown in Table II.

TABLE II.

Average Number of Wireworms per Square Metre in Weedy Fields and in Fields kept Fallow (Chuchkowo, Moscow District, July 1936).

Name of Wireworm	Arable fields kept fallow	Weedy fields
Selatosomus latus, F.	0·16–1·66	11·0
Agriotes sputator, L.	6·5–10·0	2·4

In the literature records are found that wireworms of the genus *Selatosomus* prefer hard soils, while *Agriotes* spp. prefer mellow ones (G.M.Y. 1936) ; that *Agriotes* is more numerous in arable soils, and *Selatosomus latus* in abandoned fields (Ponomarenko, 1935), etc. ; but without any explanations of these differences.

Such different relations of various insects to soil utilisation may be explained by their feeding habits. Our investigations showed that soil pests (wireworms, false wireworms and white-grubs) are able to feed not only on living plants, but also on decaying vegetation and humus (Ghilarov & Lukianovich, 1935 ; Ghilarov, 1937 ; see also Langenbuch, 1932). But not all these insects are saprophagous to the same degree. For example, among the soil inhabiting Lamellicorn larvae are to be found species feeding chiefly on decaying matter (such as various CETONIINI, *Oryctes nasicornis*, L.), which very seldom attack living plants, except when the soil is deficient in humus or moisture. On the other hand, such species as *Polyphylla fullo*, L., are prevalently phytophagous and feed on decaying plant remains only in the absence of living plants.

Most soil pests can be either saprophagous or phytophagous, but in each species there is always a significant tendency towards one or other of these feeding habits. The relationship to soil cultivation, in particular to summer fallow on which the growth of plants is kept down, cannot be the same in insects that are mainly saprophagous as in those that are mainly phytophagous. The plant-eating species find better conditions on uncultivated weedy land, where they have plant food practically always. On cultivated land the deficiency of plant food due to tillage makes conditions that are unfavourable for mainly phytophagous insects and even lethal for those that are obligatory plant-eaters.

Therefore in steppe areas the purely phytophagous larvae of *Dorcadion*, which are very abundant in uncultivated lands, decrease rapidly after tillage. In old arable fields these insects are practically absent. Contrariwise, soil pests that feed principally on decaying matter find in arable soils a favourable environment. The moisture of fallow soil (an indispensable condition for saprophagy) is higher than that of soil-bearing vegetation, where it is removed as a result of plant transpiration.

The fact that nearly always greater injury is caused by species prevalently inhabiting abandoned lands bearing vegetation than by those occurring chiefly in the older farm lands in the " chernozem " soils of the Ukraine, proves that the former are mainly plant-eaters, while the latter are mainly saprophagous.

A comparison of the damage done by the wireworms *Agriotes sputator* and *A. gurgistanus* with that due to the larvae of *Selatosomus* gives the following results. The loss of young rubber-plants (*Skorzonera tau-saghyz*) from *Agriotes*, with a density of about 14 larvae per square metre, amounted only to 10–15 per cent.; while *Selatosomus* (6·5 per square metre) destroyed about 60 per cent. of the plants (Dirsch, 1934; Ghilarov & Lukianovich, 1935).

Often we observed wireworms of the genus *Agriotes* boring into decaying roots of *Taraxacum* and *Skorzonera*, while the larvae of *Selatosomus* were to be found attacking only quite healthy plants.

During the dry periods of summer in plant-bearing lands the larvae of *Selatosomus* remain near the soil surface, where they counteract the loss of water from their bodies by feeding on roots; while *Agriotes* larvae migrate downwards into more moist strata (see also Vereshchagin, 1935).

It seems that not only in the Ukraine, but also in other countries, wireworms resembling the larvae of *Selatosomus* (with the furcated caudal part of the ninth abdominal segment well developed—urogomphi) are connected with uncultivated lands and very injurious; while wireworms with a conoidal, unfurcated ninth abdominal segment, which are less destructive to crops (principally different species of the genus *Agriotes*), are prevalent in arable lands that are periodically kept fallow.

In some localities near Moscow in weedy uncultivated lands the most abundant species is *Athous niger*, L., whose larvae are very similar to those of *Selatosomus*, while on old farm lands *Agriotes lineatus* and *A. obscurus* are more numerous. According to Langenbuch (1932), the larvae of the two latter species are mainly saprophagous.

In Middle Asia (Kazakhstan, Uzbekistan) uncultivated dry lands (where saprophagy is impossible, because the soil is too dry) are inhabited by wireworms of the genus *Pleonomus* (mainly *P. tereticollis*, Men.), which are very dangerous for " bogara " crops, *i.e.*, crops grown without irrigation. It is very difficult or even impossible to distinguish the larvae of the Asiatic *Pleonomus* from those of the European *Athous* (Troitzky & Shchegolev, 1934).

On the irrigated arable lands in Middle Asia the commonest wireworm is the practically almost harmless *Agriotes meticulosus*, Esch. (see also Rodd, Gussakovsky & Antova, 1933). It has been recorded by Bolshakov (1935) that in irrigated fields of *Skorzonera tau-saghyz*, in the patches without any plants, the larvae of *Agriotes meticulosus* remain in these areas feeding on decaying matter, while *Pleonomus* larvae migrate to the margins of the bare patches and attack the plants.

According to Lane (1931, 1935), in the Pacific North-west of the United States the most economically important wireworms of the genus *Ludius** (which resemble the larvae of the European *Selatosomus*) are restricted in their habitat to the dry land areas. Several species of the genus *Agriotes* present in the Pacific North-west have not been reported as doing damage, while the only injurious species of this group in U.S.A., *Agriotes mancus*, Say, is harmful only on the older farm lands in districts where the soil moisture seems to be higher (see also Hawkins, 1936).

The flattened area of the ninth abdominal segment and urogomphi of wireworms inhabiting hard soils may be of use for boring through such soils, and possibly this accounts for the correlation between the form of the caudal segments of wireworms and the character of their habitats and feeding habits.

All that has been said about the feeding habits of *Agriotes* larvae is entirely applicable to the false wireworms occurring mainly in arable chernozem soil in the Ukraine (*Omophlus* spp., *Podonta daghestanica*, *Opatrum sabulosum*).

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* *L. noxius*, Hyslop, *L. inflatus*, Say, *L. aereipennis*, Kby.

Analogous correlations exist between the character of the usual habitat and the feeding habits of injurious Scarabaeid larvae. The larva of *Amphimallus solstitialis* prefers uncultivated lands and is more phytophagous than the larva of *Anisoplia austriaca* that occurs almost exclusively in tillage. The larvae of *A. solstitialis*, with a density of about 0·5 per square metre, under the conditions of the Ukraine, destroy usually up to 30 per cent. of young plants of *Scorzonera tau-saghyz*, while even 4–5 larvae of *A. austriaca* per square metre only cause a loss that is quite negligible.

The feeding habits of larvae of soil pests determine the character of their habitats and the behaviour of the egg-laying adults. It is clear, for instance, why the females of *Amphimallus* deposit their eggs in weedy places and avoid plantless ones (Vodolagin, 1935), while *Anisoplia* prefers for egg-laying thoroughly ploughed fallows, etc. (see also Vassiliev, 1914).

Possibly the fact that crops are especially badly damaged by wireworms if they are sown just after the breaking of fresh ground, while on old farming soils the injury with the same degree of infestation is negligible, may be explained by a difference in the species forming the wireworm populations in cultivated and uncultivated lands.

The capacity of soil insects for saprophagy is the property that determines not only the differentiation of the injurious soil fauna of unelaborated and cultivated soils, but also the formation of natural soil-biocoenoses. In soil that is moist enough and rich in humus and other decaying matter, saprophagy gives an advantage in the struggle for life, and therefore the fauna of Scarabaeid, Elaterid, Alleculid and Tenebrionid larvae consists mainly of facultative saprophagi.

In the soils poor in decaying matter, for example sandy soils, where saprophagy gives no advantage in the struggle for life, the fauna of these insects consists of almost purely phytophagous species, such as *Selatosomus aeneus* and *Polyphylla fullo* in the Dniepr sands in the Ukraine.

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COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st July and 30th September, 1937.

Agricultural Research Service, Khartoum :—13 Diptera, 39 Parasitic Hymenoptera, 3 other Hymenoptera, 11 Lepidoptera, 1 species of Coccidae, and 20 other Rhynchota ; from the Sudan.

Mr. P. N. Krishna Ayyar :—29 Coleoptera and 150 Parasitic Hymenoptera ; from South India.

Mr. E. Ballard, Chief Plant Protection Officer :—14 Diptera, 45 Coleoptera, 18 Parasitic Hymenoptera, 2 other Hymenoptera, 22 Lepidoptera, 50 Isoptera, 1 species of Coccidae, 14 other Rhynchota, and 2 Chelifera ; from Palestine.

Dr. H. F. Barnes, Rothamsted Experiment Station :—30 Parasitic Hymenoptera ; from England.

Dr. H. Bischoff :—5 Parasitic Hymenoptera ; from Germany.

Dr. G. Bondar :—17 Diptera and 86 Coleoptera ; from Brazil.

Borough Engineer, Douglas :—1 Siricid ; from the Isle of Man.

Mr. F. Bourquin :—15 Lepidoptera ; from the Argentine.

Mr. H. E. Box :—12 Coleoptera ; from Cuba and St. Lucia.

Mr. L. L. Buchanan :—7 Coleoptera ; from Alabama and the Argentine.

Mr. E. McC. Callan :—43 Parasitic Hymenoptera ; from England.

Mr. J. Carroll :—4 Diptera ; from Ireland.

Chief Entomologist, Pretoria :—67 Coleoptera and 66 Parasitic Hymenoptera ; from South Africa.

Mr. L. D. Cleare, Junr., Government Entomologist :—12 Diptera, 19 Coleoptera, 12 Parasitic Hymenoptera, and 1 species of Coccidae ; from British Guiana.

Mr. G. H. Corbett, Government Entomologist :—69 Diptera, 64 Coleoptera, 100 Parasitic Hymenoptera and 8 cocoons, 15 other Hymenoptera, 49 Lepidoptera, 100 Isoptera, 62 Rhynchota, and 8 Orthoptera ; from Malaya.

Coryndon Memorial Museum, Nairobi :—1,500 Coleoptera ; from East Africa.

Mr. G. S. Cotterell, Government Entomologist :—20 Diptera, 28 Coleoptera, 22 Parasitic Hymenoptera, 46 other Hymenoptera, 27 Lepidoptera, 30 Thysanoptera, 3 species of Coccidae, 4 other Rhynchota, and 200 Psocidae ; from the Gold Coast.

Mr. M. Delassus :—3 Diptera and 6 Thysanoptera ; from Algeria.

Director of Agriculture, Mauritius :—52 Diptera, 2 Hymenoptera, 2 species of Coccidae, 3 other Rhynchota, and 6 Orthoptera.

Mr. H. L. Dolton :—3 Braconidae and 50 cocoons ; from England.

Mr. V. H. W. Dowson :—50 Isoptera ; from Iraq.

Mr. W. H. Edwards, Government Entomologist :—51 Coleoptera and 22 larvae, and 2 Parasitic Hymenoptera ; from Jamaica.

Dr. H. S. Evans :—6 Siphonaptera, 3 Diptera and 3 early stages, 5 Coleoptera and 4 early stages, 7 Lepidopterous eggs, 3 Rhynchota, 5 Psocidae, 13 Dermaptera, 4 Embiidae, 7 Planipennia early stages, 2 Collembola, 50 Anoplura, 25 Ticks, 7 Mites, 3 Spiders, 2 Chelifera, and 9 Worms ; from Northern Rhodesia.

Mr. J. W. Evans, Entomologist :—3 Coleoptera, 6 Parasitic Hymenoptera, 2 other Hymenoptera, 2 Lepidoptera, 7 Orthoptera, 5 Planipennia, and 7 Odonata ; from Tasmania.

Mr. J. L. Froggatt, Government Entomologist :—3 Tabanidae, 28 other Diptera, 193 Coleoptera, 14 Parasitic Hymenoptera, 10 other Hymenoptera, 19 Lepidoptera, 1 species of Coccidae, 95 other Rhynchota, 7 Orthoptera, and 3 Odonata ; from New Guinea.

Mr. J. C. M. Gardner, Systematic Entomologist, Forest Res. Inst. :—256 Parasitic Hymenoptera and 4 Lepidoptera ; from the United Provinces, India.

Dr. D. C. Geijskes :—25 Parasitic Hymenoptera ; from Holland.

Mr. F. D. Golding, Government Entomologist :—3 Tabanidae, 10 *Stomoxys*, 45 other Diptera, 9 Coleoptera, 2 Lepidoptera, 7 Thysanoptera, 14 Rhynchota, 52 Orthoptera, and 200 Collembola ; from Nigeria.

Government Entomologist, Coimbatore :—64 Diptera, 34 Hymenoptera, 29 Lepidoptera, 2 species of Coccidae, and 3 other Rhynchota ; from South India.

Government Entomologist, Lyallpur : —5 Coleoptera and 1 species of Coccidae ; from the Punjab, India.

Mr. H. Hargreaves, Government Entomologist :—15 Diptera, 47 Coleoptera, 529 Parasitic Hymenoptera and 100 cocoons, 27 other Hymenoptera, 157 Lepidoptera, 150 Rhynchota, 5 Orthoptera, and 200 Crustacea ; from Uganda.

Mr. W. E. H. Hodson :—5 Diptera ; from England.

Dr. W. Horn :—2,067 Coleoptera ; from various localities.

Messrs, A. V. Humphries, Ltd. :—8 Lepidopterous larvae ; from England.

Imperial Entomologist, New Delhi :—103 Diptera, 28 Coleoptera, 80 Parasitic Hymenoptera, 456 Lepidoptera, 2 species of Coccidae, and 15 species of Aphidae ; from India.

Institute for Plant Diseases, Buitenzorg :—60 Parasitic Hymenoptera ; from the Dutch East Indies.

Mr. W. F. Jepson :—82 Diptera ; from South Africa.

Mr. C. B. R. King, Entomologist, Tea Research Inst. :—9 Parasitic Hymenoptera and 10 Collembola ; from Ceylon.

Mr. C. D. Knight :—5 Hymenopterous early stages ; from Kenya Colony.

Dr. R. H. Le Pelley :—50 Diptera, 55 Coleoptera, and 250 Parasitic Hymenoptera ; from Java and the Philippine Islands.

Mr. C. J. Louwerens :—136 Coleoptera ; from Java.

Mrs. K. C. Mackay :—1 Tabanid ; from Ireland.

Prof. F. J. Meggitt :—5 Tabanidae, 13 other Diptera, 199 Coleoptera, 2 Parasitic Hymenoptera, 38 other Hymenoptera, 6 Lepidoptera and 8 larvae, 17 Rhynchota, 31 Orthoptera, 2 Dermaptera, and 3 Odonata ; from Burma.

Mr. A. R. Melville :—300 Parasitic Hymenoptera ; from Kenya Colony.

Dr. R. Menzel :—30 Parasitic Hymenoptera ; from Switzerland.

Dr. D. Miller, Cawthron Institute :—18 Parasitic Hymenoptera and 12 cocoons ; from New Zealand.

Mr. J. Mimeur :—2 Lepidoptera ; from Morocco.

Mr. O. Monté :—11 Coleoptera ; from Brazil.

Mr. H. M. Morris, Government Entomologist :—26 Coleoptera and 7 Lepidoptera ; from Cyprus.

Mr. R. W. Mungomery :—5 Diptera and 36 Rhynchota ; from North Queensland.

Musée du Congo Belge, Tervueren :—797 Coleoptera ; from the Belgian Congo.

Dr. J. G. MYERS :—1 Chalcid ; from Haiti.

OXFORD UNIVERSITY MUSEUM :—270 Diptera, 70 cocoons and 23 host specimens, 3,268 Parasite Hymenoptera, 450 cocoons and 176 host specimens ; from East Africa.

Mr. H. G. PALMER :—2 Coleoptera ; from England.

Mr. L. PALMONI :—50 Siphonaptera, 18 Culicidae, 645 other Diptera and 3 larvae, 16 Coleoptera, 73 Parasitic Hymenoptera, 59 other Hymenoptera, 22 Lepidoptera, 9 Isoptera, 60 Thysanoptera, 4 species of Aphidae, 1 species of Aleurodidae 32 other Rhynchota, 8 Hemimeridae, 2 Embiidae, 165 Collembola, 3 Ticks, and 10 Mites ; from Palestine.

Mr. E. F. PECK, Veterinary and Agricultural Officer :—29 *Lyperosia*, 8 Coleoptera, 100 Rhynchota, 6 Anoplura, and 100 Ticks ; from British Somaliland.

Mr. J. S. PHILLIPS :—70 Parasitic Hymenoptera ; from Fiji.

DR. S. V. P. PILL :—3 Coleoptera and 363 Orthoptera ; from South Iran.

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DR. H. PRIESNER :—7 Cecidomyiidae ; from Egypt.

PULLMAN CAR COMPANY :—10 Coleopterous early stages ; from England.

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Mr. E. R. SPEYER :—2 Syrphidae and 2 larvae ; from England.

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Dr. H. STROUHAL :—900 Parasitic Hymenoptera ; from Austria and Czechoslovakia.

Mr. V. K. SUBRAMHANYAM :—30 Thysanoptera and 100 Mites ; from Mysore, India.

Dr. A. L. TONNOIR :—250 Rhynchota ; from Australia.

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UNITED STATES NATIONAL MUSEUM, WASHINGTON :—4 Braconidae ; from the West Indies.

Dr. J. W. VAN DER LINDE :—29 Coleoptera ; from South Africa.

Dr. F. VAN EMDEN :—40 Coleoptera and 110 early stages ; from Java and Japan.

Mr. D. VESEY-FITZGERALD :—37 species of Coccidae ; from the Seychelles.

VIENNA MUSEUM :—5,280 Braconidae ; from Europe.

Mr. G. B. WALLACE :—13 species of Coccidae ; from Tanganyika Territory.

WEST JAVA EXPERIMENT STATION :—28 Coleoptera, 46 Lepidoptera, and 12 Rhynchota ; from Java.

Mr. F. G. S. WHITFIELD, Medical Entomologist :—4 Siphonaptera, 175 Culicidae and 6 early stages, 1,011 other Diptera, 6 Coleoptera, 12 Hymenoptera, and 12 Lepidoptera ; from the Sudan.

Mr. H. WILKINSON, Entomologist :—2 Diptera, 41 Coleoptera and 50 early stages, 40 Parasitic Hymenoptera, 24 Lepidoptera, 6 slides of Thysanoptera, 2 species of Coccidae, 17 other Rhynchota, 5 Psocidae, 100 Mites, 50 Parasitic Worms, and 50 Earthworms ; from Kenya Colony.

Mr. G. N. WOLCOTT :—50 Diptera and 20 Hymenoptera ; from Porto Rico.

Mrs. W. R. O. WYNN :—1 Ichneumonid ; from England.

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